

Morphological studies on some inland Rhizophoraceae

by

GEH SIEW YIN¹ ET HSUAN KENG²

I. Introduction

The family Rhizophoraceae (as Ordo Rhizophoreae) was first established by R. Brown in 1814, and includes *Rhizophora* L., *Bruguiera* Lamk., and *Carallia* Roxb. Other genera were subsequently added by Bentham and Hooker and others and the Rhizophoraceae has since been expanded to comprise 16 genera and approximately 120 species of trees and shrubs (Hou, 1958) which are pan-tropical in distribution.

The best known representatives of the family are four mangrove genera, viz. *Rhizophora*, *Bruguiera*, *Ceriops*, and *Kandelia*, which are characterized by their peculiar adaptive features of viviparous fruits, in which the seeds undergo germination on the parent plant, and by their various special roots (pneumatophores and knee roots), which enable the plants to thrive in a muddy, littoral habitat. These mangrove genera have been extensively studied by many authors. The majority of the Rhizophoraceous genera are, however, inland plants which exhibit none of these special adaptive characters and are relatively less investigated. It is because of this that the classification of the family has been subjected to much revision and rearrangement.

The present investigation is mainly confined to the species of the following 5 inland Rhizophoraceous genera, viz., *Anisophyllea*, *Carallia*, *Combretocarpus*, *Gynotroches* and *Pellacalyx*, found in Singapore and Malaysia.

Members of the inland Rhizophoraceae are usually sun-loving, gregarious, and generally found in secondary forests. Because they are normally small trees, their timbers, except for construction, possess little or no commercial value, yet from the ecological point of view they are among the important pioneer trees which prepare a suitable environment for other superior trees such as dipterocarps and others to grow.

The specimens of 8 species belonging to 5 different genera examined were partly fresh material collected in Singapore, and partly from herbarium or wood collections of the Botanic Gardens, Singapore, from Dr. T. C. Whitmore, formerly of the Forest Research Institute, Kepong, and from Dr. J. A. R. Anderson, former Conservator of Forests, Sarawak. The nomenclature of the material used follows a recent taxonomic treatment by Hou (1958).

Fresh material including leaves, stems, flowers, fruits and seedlings were preserved in formalin-acetic acid-alcohol (F.A.A.). Infiltration of the fluid was facilitated by the use of the suction pump. Material taken from the herbarium collections were first softened in a dilute solution of sodium hydroxide (5%) then thoroughly rinsed in water and stored in 70% alcohol. Wood specimens were cut into

1. Botanic Gardens, Singapore.

2. Department of Botany, University of Singapore.

small cubes and boiled for 1 ~ 2 hours to remove the air, transferred to 30%–40% hydrofluoric acid for periods of one month or longer, washed overnight in running water and then stored in glycerin-alcohol.

Serial sections of twigs, petioles, leaves, flower buds and mature flowers were obtained by the paraffin method. Dehydration and embedding were carried out by the tertiary butyl alcohol series in accordance with the method described by Johansen (1940). Sections of 8–15 μ were obtained by means of the rotary microtome, and these were then stained with a safranin and fast-green combination.

Semi-permanent preparations of pollen grains were obtained by scraping pollen grains from recently dehiscent anthers into lactophenol, and sealing the mounted slides with nail polish.

Cleared leaves and floral parts were prepared according to a modification of Foster's (1949) and Arnott's (1959) methods.

Transverse, tangential, and radial longitudinal sections of wood material were obtained with a sliding microtome. The sections were stained in safranin, dehydrated through the xylene-alcohol or tertiary-butyl-alcohol series and mounted in euparal. Fragments of wood were macerated in Jeffrey's nitric-chromic acid mixture.

II. External Morphological Observations

External morphological observations on fruits, seeds and seedlings of various genera and species were made during the course of this study.

Fruits of *Anisophyllea disticha*, *Carallia brachiata*, *Gynotroches axillaris*, *Pellacalyx axillaris* and *P. saccardianus* were collected and the following observations recorded. Attempts to germinate the seeds from these fruits proved to be unsuccessful, although several batches of seeds (8 for *Anisophyllea disticha*; 30–40 for the other species) in different media (soil, sand, filter paper) and under light and dark conditions were experimented with. Consequently only the seedling stages of two species, *Anisophyllea disticha* and *Gynotroches axillaris*, found in the field are described below. Fruits of *Combretocarpus rotundatus* are described from herbarium and pickled material obtained from Kuching, Sarawak and from the Forest Research Institute, Kepong, Malaysia.

a. FRUIT

Genera of the Rhizophoraceae appear to differ considerably in fruit structure. Baccate fruits are present in *Carallia* (Fig. 3 C), *Gynotroches* (Fig. 5 C) and *Pellacalyx* (Fig. 6 C), while *Anisophyllea* (Fig. 2 C) produces drupaceous fruits and *Combretocarpus* (Fig. 4 D) dry, indehiscent, winged fruits. Plants of the mangrove genera, *Rhizophora*, *Bruguiera*, *Ceriops* and *Kandelia*, are well-known for their peculiar one-seeded, viviparous fruits.

The fruits of the Gynotrocheae vary in size from small and globular in *Carallia brachiata* (2.5–3.5 mm across) and *Gynotroches axillaris*, to large and turbinate in *Pellacalyx axillaris* and *P. saccardianus* (1–1.5 cm across). The fruits of these plants are further differentiated by the glabrous character of the former two species and the puberulous exterior of the *Pellacalyx* fruits.

The fruits of *Carallia brachiata* are many-seeded with the light-brown seeds embedded in an axile placenta. The pericarp changes from green, through translucent pink to red as the fruit matures. *Gynotroches axillaris* produces similar

fruits which ripen to a shiny black on maturity. The fruits borne by *Pellacalyx axillaris* and *P. saccardianus* are approximately four to five times the size of the other two genera, and are very similar to one another in size; *P. saccardianus* can, however, be distinguished by its four-shouldered berries which are situated on longer stalks and are less densely puberulous than those of *P. axillaris*. Mature fruits of *Pellacalyx* are yellowish-green in colour.

The fertilised ovary of *Anisophyllea disticha* develops into a succulent drupe which ripens from pale pink to bright red. These fruits are often found in pairs or singly, on the underside of the pendent branches. The succulent mesocarp encloses a yellowish-brown stone which is acute at both ends and ridged longitudinally; these ridges are obvious in dried specimens of the fruits. *Combretocarpus rotundatus* produces a winged fruit in contrast to the other members of the family. There are usually three, less often four, membranous extensions of the pericarp which are delicately transversely veined. The single enclosed seed is spindle-shaped and very slender.

The fruits of all the species examined possess persistent calyx lobes. These lobes are situated above the pomaceous fruits which are formed by inferior or half-inferior ovaries except in *Gynotroches axillaris* where it is found below the berry. Very often, remains of stamens and style are also persistent on the fruit but the petals of all species are caducous. The persistence of the calyx is also notable in the fruits of the mangrove genera where they often become accrescent. There is hardly any other common feature between the fruits of the tidal and inland species than this.

b. SEED

Plants of the Gynotrocheae are characterized by comparatively small but several to numerous seeds embedded in pulpy placentae of baccate fruits. Each locule of the ovary in *Carallia brachiata* houses two ovules, while in the other two genera, there are several to many ovules per locule. The ovules of *Pellacalyx* species are arranged in fascicles of 8–25 attached to an axile placenta while those of *Gynotroches axillaris* are found embedded in a mass of placental and endocarpic tissue.

The seeds of these species are light yellowish-brown to dark brown in colour, and the testa is often crustaceous or sometimes coriaceous. Endosperm is always present surrounding the embryo which is axile, linear and practically extending from one end of the seed to the other.

Both *Combretocarpus rotundatus* and *Anisophyllea disticha* have fairly large single-seeded fruits. In *C. rotundatus* the pendulous seed lies in the centre of the fruit attached to the apex of the locule and is enclosed by a thin dry pericarp which is extended externally into 3–4 wings. The embryo is linear and cylindrical, and sections of the fruit reveal the presence of two distinct cotyledons and a fairly long hypocotyl; the plumule within the cotyledons is rudimentary. Surrounding the embryo is a structurally differentiated endosperm which is composed of densely cytoplasmic and more darkly stained cells. There is a clear demarcation between the embryo and its surrounding tissue, contrary to Hou's observation (1958) that the embryo and endosperm form a solid whole and are not differentiable under the microscope.

Freehand and microtome sections of the fruit and seed of *Anisophyllea disticha* at different stages show that the embryo is yellowish-white, axile, linear and embedded in a tissue which is endospermous in nature (Fig. 2 C 1 to C 5).

Hou (1958), possibly from dried material, has described the embryo and its enveloping tissue as forming a solid unity. This was not found to be so in the fresh specimens examined, as in all cases the embryo proper was quite naturally separable from its surrounding tissues. In the young seed, the endosperm takes up most of the space with the embryo confined to the apical portion, but as the seed matures, the embryo gradually occupies the entire central region, at the expense of the endosperm. Thus in longitudinal sections of a mature seed, it reveals the embryo as a terete structure extending almost the entire length of the seed. At the apical portion of the embryo two protuberances are observed which can be interpreted as cotyledons*. The rest of the embryo is a solid cylindrical structure with a sheath of small-celled vascular tissue separating the cortical from the central region. Between the cotyledons is the plumule which elongates into a young shoot and later bears the scale-like cataphylls of the seedling.

The seeds of the mangrove members of the Rhizophoraceae are distinguished by their conspicuous hypocotyls which develop while the fruit is still attached to the parent plant. In *Rhizophora* and *Bruguiera* the two cotyledons are connate into a sheath and surround the plumule, serving to assimilate nutrients from the endosperm for the developing embryo. This form of cotyledons is not confronted in the inland genera and is absent in *Anisophyllea disticha* where the entire, undifferentiated embryo is embedded in endospermous tissue.

c. SEEDLING

Although usually abundant fruits and seeds are produced by individual plants belonging to the inland Rhizophoraceous genera, the number of seeds which actually germinate appears to be very small indeed. Therefore, seedlings of these species are not commonly found on forest floor. Fresh seeds of several species (including *Carallia*, *Gynotroches*, *Pellacalyx*, *Anisophyllea*) collected in the field mostly failed to germinate in the laboratory and consequently only seedlings of the following two species are described.

Germination in *Anisophyllea disticha* seed is distinctly hypogeal (Fig. 7). The seed lies prostrate on the ground at first, then is carried downwards together with the radicle as the latter penetrates the soil, and soon produces lateral roots. Roots are formed from both ends of the seed, with the plumular end producing a less developed root system. The cotyledons and hypocotyl do not emerge outside the seed, but the plumule elongates into a strong cylindrical stem portion bearing small scale-like cataphylls before the first whorl of lateral branches is produced.

Gynotroches axillaris seed germinates into a seedling which does not produce cataphylls. Cotyledons have not been found on any of the seedlings observed, thus it is not possible to determine if germination was epigeal or hypogeal (Fig. 8). However, since in the mangrove genera the first green leaves are not cotyledonary, and the germination of *Anisophyllea* is hypogeal, it is perhaps reasonable to presume that the germination in *Gynotroches* and other inland plants may also be hypogeal. Seedling leaves of *G. axillaris* resemble very closely the mature leaves in their general shape, colour, texture and especially in venation. Another prominent feature

* The seed structure of *Barringtonia* as observed by Payens (1967), in general, is very similar to that of *Anisophyllea disticha*; in both cases, the embryos are not clearly differentiated into plumule, cotyledons and hypocotyl. The two protuberances at the apical end of the embryo of *Barringtonia* are considered by Payens to be scales, not cotyledons, on account of their spiral arrangement and the presence of axillary meristems. Those at the apical end of the embryo of *Anisophyllea disticha*, however, are strictly oppositely arranged, therefore can be reasonably interpreted as cotyledons.

is the conical interpetiolar stipules which cover the apical developing buds of the plants; the stipules in the Rhizophoraceae overlap one another leaving one free margin on each side, except in the case of *Pellacalyx* where the stipules are flat as in most Rubiaceae. The presence of such overlapping stipules may hence be used as a guide for identifying Rhizophoraceous seedlings, except in *Anisophyllea* and *Combretocarpus* which are exstipulate.

III. Anatomical Studies

Serial sections were made of fresh specimens of the stem, wood, leaf, petiole and flowers of *Anisophyllea disticha*, *Carallia brachiata*, *Gynotroches axillaris*, *Pellacalyx axillaris* and *P. saccardianus* collected in Singapore, and of herbarium collections of the flowers of *Combretocarpus rotundatus* and the wood of *Anisophyllea corneri*, *Carallia eugenioidea* and *C. rotundatus* obtained from Dr. J. A. R. Anderson, Sarawak and from Dr. T. C. Whitmore, Kepong, Malaysia.

A brief summary of the anatomical details of the leaf-blades, petioles, stems, woods, flowers and pollen-grains of the species investigated is presented below.

a. LEAF-BLADE (Table 1; Fig. 15)

(1) *Stomata*. The stomata in the species of the Rhizophoraceae investigated belong to the ranunculaceous or anomocytic type (Metcalf & Chalk, 1950), i.e. the epidermal cells surrounding the two guard cells are indistinguishable from the other epidermal cells; sometimes, however, the cells around the stomata are more oblong than their neighbouring cells. Stomata are confined to the lower leaf surface only.

(2) *Epidermis*. The upper epidermis varies from the uniseriate in *Anisophyllea disticha* and *Carallia brachiata*, to 2–5 layered in *Gynotroches axillaris*, *Pellacalyx axillaris* and *P. saccardianus*. The outermost layer of a multiple epidermis resembles the ordinary uniseriate epidermis in having a cuticle (absent in *P. axillaris*), while the inner layer or layers (or the hypoderm) are composed of larger cells which do not contain chloroplasts, and commonly serve as a water storage tissue. Among the hypodermal cells are frequently large mucilage producing cells which are especially conspicuous in *P. axillaris*. The thickest hypoderm, of 3–4 layers, is found in *P. saccardianus*.

The lower epidermis in all the species examined is single-layered. It is covered by a thin cuticle except in *Carallia brachiata* and *Pellacalyx axillaris* where it is nearly absent.

Cork-like warts occur as small black dots on the lower surface of *Carallia brachiata*, while tufted trichomes are present especially on the abaxial surfaces of *Pellacalyx* species. Crystalliferous inclusions in the form of druses are usually present in the upper epidermal cells of *C. brachiata*.

In contrast to the thin cuticle present in the inland genera, the mangrove species are generally covered by a thick cuticle which may be composed of two distinct layers. Multiple epidermis is also common among the mangrove genera although species of *Bruguiera* may have a uniseriate epidermis. The number of layers in the hypodermis has been directly correlated to the concentration of salt in the water where the plants are growing, in the case of *Rhizophora mangle* Linn. (Bowman, cited in Metcalfe & Chalk, 1950).

(3) *Mesophyll*. The mesophyll is differentiated into palisade and spongy tissues. In *A. disticha* the leaf is isobilateral, and the single-layered palisade is distinguished from the spongy parenchyma only by nature of its more longitudinally elongated axis. *C. brachiata* also shows a one-layered palisade tissue which is distinct from the spongy mesophyll and separated from it by 1–2 layers of parenchyma cells with tanniferous inclusions. The other species investigated have 2–4 palisade layers which are closely packed in the first layer but become more loosely arranged, and scarcely distinguishable from the spongy mesophyll in the case of *P. saccardianus*. Palisade cells of *P. axillaris* are very much narrower and anticlinally elongated than the other cells of the mesophyll.

The number of cells in the spongy mesophyll ranges from 6–17 rows in the species examined. *A. disticha* and *P. axillaris* both have approximately 6 rows of cells which are more compactly arranged in the former, but include extensive air-spaces in the latter. In *G. axillaris* the spongy mesophyll cells are small in size and loosely arranged. The lower 3–5 layers of cells are larger and more compact in arrangement forming a pseudo-hypodermis, which as defined by Metcalfe and Chalk (1950) is formed of cells not aligned with the epidermal cells and ontogenetically not derived from them. Mucilage cells are also observed in the pseudo-hypodermis.

Cells of the spongy mesophyll in *C. brachiata*, *G. axillaris* and *P. saccardianus* contain darkly stained, probably tanniferous substances. These are found in the first 2–3 layers of the spongy mesophyll in *C. brachiata*, in the last 2–3 layers beneath the lower epidermis in *P. saccardianus*, and scattered all over the mesophyll in the case of *G. axillaris*. Druses are also found occasionally in the parenchyma cells of all the species examined.

The proportion of spongy mesophyll in relation to the total leaf thickness, in average, is found as follows: — *A. disticha* 72%; *C. brachiata* 75%; *G. axillaris* 69%; *P. axillaris* 63%; *P. saccardianus* 57%. Thus, a well-developed spongy mesophyll is present in these species.

(4) *Vascular Bundles*. The mid-rib bundle is identical to and a smaller version of the median petiolar bundle in all the species under observation. The vascular bundles of the leaf blades are of the collateral type with xylem on the adaxial side and phloem below it, facing the lower epidermis. The larger veins extend from the upper epidermis or hypodermis to the spongy mesophyll, while the smaller veins are present only in the spongy tissue.

The larger vascular bundles are completely encircled by two types of bundle sheaths. The inner sheath is composed of thick-walled sclerenchymatous cells and this is overlaid by a single layer of parenchymatous tissue. Sclerenchyma frequently encloses the smaller veins of the leaf lamina which may be composed only of xylem elements. Phloem cells are absent from vein endings which are composed mainly of elongated tracheids surrounded by a parenchymatous bundle sheath.

Bundle sheath extensions are not well-developed in the inland species examined, and this is probably due to the increase of the thickness of the spongy parenchyma as suggested by Wylie (1943).

(5) *Sclereids*. Sclerenchymatous idioblasts are notably absent in the species investigated in contrast to the well-developed H-shaped sclereids in the palisade and variously branched idioblasts in the spongy mesophyll of *Rhizophora* species. Solitary sclerenchymatous cells have also been recorded in the spongy mesophyll of *Poga oleosa* by Schimper (1898).

TABLE 1
COMPARISON OF THE COMPOSITION AND RELATIVE AMOUNT OF THE
DIFFERENT TISSUES IN THE LEAVES OF INLAND RHIZOPHORACEAE

Species	Total leaf thickness (μ)	Cuticle	Epidermis		Palisade		Spongy	
		Thickness (μ)	No. of layers	Thickness (μ)	No. of layers	Thickness (μ)	No. of layers	Thickness (μ)
<i>Anisophyllea disticha</i>	..	2	1	16.5	1	33~35	5~7	84~106
<i>Carallia brachiata</i>	..	2~4	2	65~73	1~2	33~42	11~14	315~350
<i>Gynotroches axillaris</i>	..	1~2	2~4	120~132	1~2	33~37	8~12	250~280
<i>Pellacalyx axillaris</i>	..	0	2~4	45~60	2~3	40~60	6~9	140~175
<i>Pellacalyx saccardianus</i>	..	2~3	3~5	65~80	2~5	60~75	9~15	210~280

b. PETIOLE (Fig. 16)

Serial sections made through the distal end of the petiole, immediately below the lamina, show that the main vascular strand in this region is mostly U-shaped. The two margins of the median bundle have a tendency to curve inward in *C. brachiata* and in *Pellacalyx* species. The median strand of *G. axillaris* is a shallow crescent-shaped structure with another small strand fitting into the hollow of the crescent. There is no sclerenchymatous tissue surrounding the vascular strands, and 1–3 accessory bundles may be found on either side of the main trace.

The petiole of *P. axillaris* is characterized by the presence of large mucilaginous cells in the peripheral region of the cortex. Darkly stained amorphous inclusions and, occasionally, druses are present in the parenchymatous tissue of the cortical region of the four other species.

c. STEM (Fig. 17)

The young branches are oblong or elliptical in transverse section. The outer surfaces of the stems are glabrous in *C. brachiata* and *G. axillaris*, but possess trichomes in the case of *A. disticha*, *P. axillaris* and *P. saccardianus*. The epidermal cells are covered by a thin cuticle and the cortex is composed of closely arranged ground tissue. Many of the cortical cells in the species investigated contain darkly stained inclusions. A continuous ring of sclerenchyma forming the pericycle surrounds the vascular cylinder in *A. disticha*, and is absent in the other species. The vascular bundles are collateral, with phloem surrounding the xylem cylinder. The pith is very wide in all cases and is composed of thin-walled cells which are larger in the central region. In the older branches of *Gynotroches* and *Pellacalyx* species, the central pith cells disintegrate leaving a characteristic hollow, which is one of the field characters utilized in identifying these two genera. Cork formation is sub-epidermal in origin.

The nodal structure in this family is trilacunar and many-traced, and agrees with the observations by Sinnott (1914). The Rhizophoraceae has been included customarily under the Myrtales which, however, is characterized by unilacunar nodes.

d. WOOD ANATOMY (Tables 2 & 3; Figs. 18 & 19; Plate 2)

The wood structure of the five genera examined fall in harmoniously with one another in most features. Except that *Pellacalyx* exhibits vessels with opposite pitting to the ray cells and has the tendency for the pore clusters to be tangentially arranged, and the occurrence of scalariform pitting in *G. axillaris*, there is no sharp demarcation in the wood anatomy of the species investigated.

Growth rings are indistinct in members of the Rhizophoraceae and the wood is commonly diffuse porous. The pores are solitary (especially in *Anisophyllea*), or arranged in pairs, or in clusters (tangentially arranged in *Pellacalyx*). Pores are usually scanty in *Anisophyllea* and *Combretocarpus* (3–6/mm²) but more abundant in *Gynotroches* where they may number up to 25–30/mm². The pores are mostly spherical in outline and the walls are rather thin and evenly thickened. The largest pores (up to 350 μ) are found in *Anisophyllea* and *Combretocarpus*, while in the other genera they are small to medium-sized. The length of the vessel members range from medium-sized to very long in *C. brachiata* (to 1400 μ).

Pits to ray cells are generally oval and alternate in arrangement, but in *G. axillaris* they are exclusively scalariform and elongate, while in *Pellacalyx* they are opposite and angular.

TABLE 2

SUMMARY OF WOOD ANATOMY CHARACTERS OF THE INLAND
GENERA OF RHIZOPHORACEAE

Character	<i>Anisophyllea</i>	<i>Carallia</i>	<i>Combretocarpus</i>	<i>Gynotroches</i>	<i>Pellacalyx</i>
<i>Vessel member</i>					
1. Arrangement	..	Solitary or paired 6-10 per mm ²	Mostly solitary 3 per mm ²	Solitary or 3-5 18-25 per mm ²	Clusters of 2-5 15-18 per mm ²
2. Abundance	..	Round or spherical (D.)	Spherical (D.)	Angular (D.)	Angular (D.)
3. Pore outline	..	(L.)	(L.)	(L.)	(L.)
4. Diameter and length	..	105 μ	180 μ	140 μ	230 μ
lowest average	..	620 μ	350 μ	450 μ	615 μ
mean of averages	..	160 μ	380 μ	150 μ	145 μ
highest average	..	230 μ	420 μ	200 μ	193 μ
5. Pits to ray cells	..	1,155 μ	Alternate; oval	Scalariform	Opposite; angular
6. Perforation plate	..	Alternate; oval	Simple	Simple	Simple
7. End-wall	..	Simple or multiple Oblique-long caudate	Oblique	Oblique	Oblique
<i>Wood fibre</i>					
8. Wall thickness	..	Thick-walled	Thick-walled	Thick-walled	Thick-walled
9. Length	..	395 μ	1,500 μ	980 μ	1,155 μ
lowest average	..	908 μ	1,760 μ	1,350 μ	1,880 μ
mean of averages	..	1,105 μ	2,800 μ	1,850 μ	2,315 μ
highest average	..				
<i>Wood ray</i>					
10. Krib's Type	..	Heterogeneous IIa	Heterogeneous IIa	Heterogeneous IIa	Heterogeneous IIa
11. Uniseriate rays (av. height)	..	8-10 cells	12 cells	4-10 cells	10 cells
12. Multiseriate rays (av. width)	..	12-14 cells	5 cells	28-30 cells	8 cells
<i>Wood parenchyma</i>					
13. Distribution	..	Paratracheal confluent and metatracheal banded.	Paratracheal confluent and metatracheal banded.	Paratracheal confluent or aliform.	Paratracheal confluent.

TABLE 3
SUMMARY OF WOOD ANATOMY CHARACTERS OF THE TRIBES OF
RHIZOPHORACEAE

Character		Anisophylleae		Gynotrocheae		Rhizophoreae	
<i>Vessel member</i>							
1.	Arrangement ..	Often solitary, some- times paired.		Solitary or more often in pore multi- ples of 2-5.		Solitary or in multi- ples of 2-14.	
2.	Abundance ..	2-5 per mm ²		7.25 per mm ²		5-35 per mm ²	
3.	Diameter and length	(D.)	(L.)	(D.)	(L.)	(D.)	(L.)
	lowest average ..	150 μ	380 μ	116 μ	584 μ		
	mean of averages ..	292 μ	483 μ	152 μ	671 μ		
	highest average ..	347 μ	738 μ	209 μ	720 μ		
4.	Pits to ray cells ..	Alternate; oval		Alternate oval or scalariform or oppo- site angular.		Scalariform.	
5.	End wall type ..	Oblique-long caudate		Oblique		steeply inclined taper- ing ends.	
<i>Wood fibre</i>							
6.	Wall thickness ..	Thick		Thick		Thick	
7.	Length						
	lowest average ..	1,350 μ		1,014 μ			
	mean of averages ..	1,813 μ		1,385 μ			
	highest average ..	2,550 μ		1,740 μ			
<i>Wood ray</i>							
8.	Krib's Type ..	Heterogeneous II _a		Heterogeneous II _a		Heterogeneous Type II _a or Homogeneous (<i>Rhizophora</i>)	
9.	av. length of uniseriate rays	13 cells		9 cells			
10.	av. width of uniseriate rays	6 cells		10(-26) cells		3-6 cells	
<i>Wood parenchyma</i>							
11.	Distribution ..	Apotracheal or paratracheal		Paratracheal confluent		Scanty vasicentric	

Perforation plates are simple, or rarely, multiple in *Anisophyllea*. End walls are oblique and long caudate in *Anisophyllea* or oblique with less pronounced prolongations in others.

Wood fibres are thick-walled in all species examined, with a range in length of extremely short (320 μ in *C. brachiata*) to very long (2,800 μ in *Combretocarpus*).

Wood rays are consistently heterogeneous of Krib's Heterogeneous Type II_a. Uniseriate rays may be present as 2-3 cells or 28 cells (in *Gynotroches*) but are more often 4-10 cells high in *Gynotroches*. Multiseriate rays are commonly 100 or more cells high, to over 400 cells in *Carallia*. Cells of the rays may contain amorphous depositions in species of all the genera, and are most abundant in *Carallia*, but rarely found in *Pellacalyx*.

Wood parenchyma is often paratracheal confluent in *Anisophyllea*, *Combretocarpus*, *Carallia* and *Pellacalyx*, and metatracheal bands are in addition, present in the former three genera. *G. axillaris* shows a tendency towards aliform arrangement of the axial parenchyma as well as the characteristic paratracheal confluent distribution of *Anisophyllea*, *Combretocarpus* and *Gynotroches*.

Among the wood specimens of the various species examined, those of the following three are investigated for the first time.

- (1) *Anisophyllea corneri* D. Hou
- (2) *Carallia eugenioidea* King
- (3) *Pellacalyx saccardianus* Scort.

The main evolutionary trends of wood anatomy characters (pertinent to the wood anatomical characters of the Rhizophoraceae) are summarised in Table 4.

TABLE 4

SUMMARY OF EVOLUTIONARY TRENDS OF WOOD ANATOMY CHARACTERS

Character	Primitive	Intermediate	Advanced
1. Wood porosity ..	diffuse-porous	semidiffuse-porous	ring-porous
2. Vessel elements			
(a) Arrangement ..	solitary	paired	clustered in pore multiple
(b) Outline in t.s. ..	angular		oval or rounded
(c) Diameter ..	very small		very large
(d) Length ..	very long		very short
(e) Perforation plate ..	Scalariform with many bars	reticulate	simple
(f) End-wall ..	very oblique, long caudate	oblique, short caudate	horizontal
(g) Pits to ray cells ..	Scalariform, elongated	opposite; transitional; oval	alternate; rounded.
3. Wood fibres			
(a) wall thickness ..	very thin		very thick
(b) length ..	very long		very short
4. Wood rays			
(a) Krib's Type ..	Heterogeneous Type I	Heterogeneous Type IIa	Heterogeneous Type III
(b) Length of uniseriate rays	very long		very short
(c) Width of multiseriate rays	very broad		very narrow
5. Wood parenchyma			
(a) Distribution ..	diffuse-scanty	paratracheal	apotracheally banded

Following the putative phylogenetic trends (Carlquist 1961), the vessel members of the Rhizophoraceae may be considered advanced in the possession of simple perforation plates. Although the lengths and widths of the vessels in the genera investigated do not differ greatly, it is evident that *Carallia* possesses the longest vessel element length and the narrowest pore diameter, while *Anisophyllea* and *Combretocarpus* show more advanced, broader and shorter vessel members. A further advanced feature lies with the occurrence of alternately arranged pits to contiguous ray cells, but this character is not common to all five genera; *Gynotroches* shows a primitive scalariform pattern, while *Pellacalyx* possesses opposite pits, which condition is considered intermediate between those found in

Gynotroches on the one hand, and *Anisophyllea*, *Combretocarpus* and *Carallia* on the other. In the arrangement of the pores, the solitary condition, often found in *Anisophyllea* is a less evolved condition which apparently progresses through that found in *Carallia* and *Gynotroches* to the pore clusters of 2–5 found in *Pellacalyx*.

The longest wood fibre lengths are found in *Combretocarpus* (2800 μ), whereas the shortest in *Carallia* (395 μ). In this instance therefore, the wood of *Carallia* shows a more advanced character in contrast to its other more primitive vessel elements.

Wood rays of the genera studied are uniformly heterogeneous of Krib's Type IIa. The multiseriate rays are broad to very broad (28–30 cells) in *Gynotroches* and generally over 100 cells high. The highest multiseriate rays are found in *Carallia* (up to 500 cells). Uniseriate rays are shortest on the average in *Gynotroches* and longest in *Anisophyllea* in contrast to the heights of multiseriate rays found in the respective genera.

All members of the five genera show a tendency towards a paratracheal confluent arrangement of wood parenchyma, which is considered an intermediate condition in wood parenchyma phylogeny. Metatracheal bands also occur in *Anisophyllea*, *Combretocarpus* and *Carallia*.

From the data obtained, it is difficult to consider any one genus as more advanced than the other. *Anisophyllea* and *Combretocarpus* probably show a slight advantage in the number of advanced features than the other genera, but on the other hand, these features alone appear to be insufficient to consider that these two genera are phylogenetically more evolved.

According to the observations of Marco (1935) and Metcalfe and Chalk (1950), the members of the mangrove Rhizophoraceae, likewise, show a mixture of advanced and primitive wood anatomy features, but in this group, the primitive characters are more in preponderance, e.g. scalariform pitting on the lateral walls, very oblique end walls, and scanty wood parenchyma. The genus *Rhizophora* seems more advanced than the other three genera of the mangrove Rhizophoraceae in the possession of homogeneous wood rays.

Considering the wood anatomical features of the family Rhizophoraceae as a whole, the mangrove members which constitute the tribe Rhizophoreae may be regarded as the most primitive, and the inland members, especially *Anisophyllea* and *Combretocarpus* which constitute the tribe Anisophylleae, the most advanced.

e. FLOWER AND POLLEN GRAINS

The inland Rhizophoraceae produce axillary flowers either in condensed clusters (in *Gynotroches* (Fig. 5), *Carallia* (Fig. 3; Plate 1) & *Pellacalyx* (Fig. 6; Plate 1)) or in fascicles or racemose inflorescences (in *Anisophyllea* (Figs. 1 & 2) & *Combretocarpus* (Fig. 4)). In contrast, genera of the mangrove Rhizophoreae exhibit paired or cymose arrangement of the flowers. The basic inflorescence structures of the family, nevertheless, are probably cymose in nature.

The accessory floral parts are always valvate in aestivation and vary in number from 3–4 (in *Anisophyllea*, *Combretocarpus*) to 4–15 (in *Rhizophora*, *Bruguiera*). The sepals are always connate at the base into a calyx-tube with triangulate or linear calyx-lobes, each of which receives a constant supply of a single vascular trace. The petals are often clawed in *Gynotroches*, *Carallia* and *Pellacalyx*, and apically fringed in various degrees. In *Anisophyllea* and *Combretocarpus* the petals are deeply and evenly 3–5 lobed, or entire, while in the mangrove Rhizophoreae the petals are entire or bi-lobed and often associated with special

appendages. The stamens are twice the number of the petals in the inland Rhizophoraceae, and may be arranged in a single whorl around a crenulate or lobed disc, or be attached to a calyx tube as in *Pellacalyx* species. The filaments are unequal in length in *Carallia brachiata* and *Pellacalyx* species (the anti-sepalous ones being shorter in *C. brachiata* and longer in *P. axillaris* and *P. saccardianus*). Among the mangrove genera, the filaments of *Rhizophora* species are extremely short, and those of *Bruguiera* are arranged in unequal pairs which are embraced by the petals. The filaments of stamens in the other Malayan genera of Rhizophoraceae are more or less equal in length. The anthers are generally small, 4-locular, dorsifixed and dehiscing longitudinally and introrse. Anthers of *Rhizophora* deserve special mention as they are large and multiloculate, producing clouds of pollen at anthesis.

The microspore mother cells in a developing anther are enveloped by 5 layers: an inner tapetum, an outer epidermis and three intermediate layers. The layer immediately underlying the epidermis produces 'fibrous' thickenings of the wall which is so characteristic of the endothecial layer, and which presumably facilitates pollen dispersal (Eames, 1961).

Following meiosis of the microsporocytes the tapetal and middle layers disintegrate and are absorbed by the developing pollen grains so that at maturity, only a spirally thickened endothecium and epidermis remain. In all the six species the septum between the locules of each half-anther usually ruptures before the pollen is released by a longitudinal line of dehiscence. The cells around the region of dehiscence are smaller, isodiametric, and thin-walled, and the epidermal cells are inconspicuous above this region.

According to Erdtman (1952) the pollen grains of Rhizophoraceae are 3(–4)-colporoidate, colporate, oblate-spheroidal to subprolate, and with finely reticulate or indistinct exine pattern. Table 5 shows the specific pollen type in the listed species. The pollen grains of the species listed are more or less similar in appearance. There is no pronounced difference between the pollen structure of the species of the three genera, and pollen morphology in this case does not seem to assist in the identification of the members of the family.

TABLE 5
POLLEN GRAINS OF THE RHIZOPHORACEAE

Species	Size	Shape	Exine pattern
<i>Anisophyllea disticha</i> ..	19.8 μ x 16.5 μ	Subprolate	Indistinct
<i>Combretocarpus rotundatus</i>	24 μ x 10.6 μ	Subprolate	Indistinct
<i>Carallia brachiata</i> ..	16.5 μ x 15 μ	Prolate-spheroidal	Finely reticulate
<i>Gynotroches axillaris</i> ..	10.5 μ x 8.6 μ	Subprolate	Finely reticulate
<i>Pellacalyx axillaris</i> ..	12 μ x 10.5 μ	Subprolate	Indistinct
<i>Pellacalyx saccardianus</i> ..	13.2 μ x 9.9 μ	Subprolate	Indistinct
<i>Bruguiera</i> ..	21 μ x 17 μ	Subprolate	Finely reticulate
<i>Ceriops candolleana</i> ..	15 μ x 15.5 μ	Oblate-spheroidal	Finely reticulate
<i>Rhizophora mucronata</i> ..	25 μ x 21 μ	Subprolate	Finely reticulate

The compound gynoecium is generally 2–12-loculate. The floral vasculature of the plants show the presence of two series of traces, an outer series which supplies the calyx, corolla and androecium, and an inner series which comprises the gynoecial vasculature. Traces supplying the carpels diverge into the ovules as well as ramify in the carpellary walls before supplying the style or styles of the various species.

The ovary is usually inferior (Figs. 9, 11, 12, 14), rarely superior (e.g. in *Gynotroches* (Fig. 13)). Internally the gynoecium is divided by septa into as many locules as the number of carpels. The ovules, varying from 1–2 to numerous per locule, are pendulous and attached to an axile placenta.

The placentation in the Rhizophoraceae is generally described as axile, but serial sections of flower buds show that the uppermost portions of the syncarpous ovary of *Combretocarpus* (Fig. 12) and *Gynotroches* (Fig. 13) are unilocular, indicating the parietal condition.

In *Combretocarpus* the carpels are fused by their ovarian regions but the styles and stigmas are separate. Each style is grooved longitudinally on its ventral (inner) surface, and as sections are taken down the lengths of the styles, there is evidence of lateral concrescence of the adjacent margins of the styles. This condition finds its equivalent in the corresponding junction of the margins of a whorl of open conduplicate carpels. As a result, the lower part of the style and the upper one-third of the inferior ovary are unilocular, while sections lower down show the typical plurilocular syncarpous ovary with axile placentation.

In *Gynotroches* the style is simple and hollow in its lower half. This hollow cavity leads down to the upper part of the superior ovary, and sections taken at this point reveal a single locule deeply subdivided by projecting partitions of the conjunct margins of each carpel, which do not meet in the centre. The lower part of the ovary is by contrast, divided into 4–5 chambers as a result of the union of the partitions. In the older flowers the axile condition is more pronounced and the parietal arrangement becomes somewhat obscure.

Attempts to draw any conclusion about phylogenetic relationships of axile and parietal placentation require great caution (Puri, 1952). The two conditions may have arisen independently from marginal placentation or one condition may have arisen from the other. The situation occurring in *Combretocarpus* and *Gynotroches*, nevertheless, seems to suggest that there is possibly a general trend from parietal to the commonly axile placentation (see Gundersen, 1939) in the Rhizophoraceae.

Each ovule has two integuments. In *Gynotroches*, *Carallia*, and *Pellacalyx*, the outer integument develops thick walls and becomes crustaceous while the inner integument is membranous. In *Anisophyllea disticha*, the outer is also composed of thick-walled cells which is lined by a thin-walled, 1–2-layered, inner integument. In *Combretocarpus rotundatus* however, the outer integument is composed of 3–4 layers of cells with less conspicuously thickened walls in contrast to the single-layered inner integument.

In the mangrove and in some inland Rhizophoreae, a simple style is found which is connected to a simple or lobed stigmatic crest. In *Anisophyllea* and *Combretocarpus* however, as described before, 3–4 styles are present each of which shows a ventral groove running from the apical stigmatic surface to the ovary. The styles of *Carallia brachiata*, *Gynotroches axillaris*, and *Pellacalyx* spp. have a styler canal running from stigma or upper styler region to the ovary.

IV. Taxonomic Considerations

The subdivision of the family Rhizophoraceae has been a subject of controversy ever since it was established by R. Brown in 1814. Four major systems of classification of the family have so far been proposed. They were by Hooker (in Bentham and Hooker f., 1862–67), Schimper (1898), Ridley (1922), and Melchior (1964).

Following Hooker's system, the family includes 3 tribes, namely:

- (1) the *Rhizophoreae*, members of the mangrove genera (*Rhizophora*, *Bruguiera*, *Kandelia*, etc.), which exhibit inferior ovary, single style, exalbuminous macropodous embryo, viviparous germination, and opposite, entire, glabrous, stipulate leaves.
- (2) the *Legnotidae* which includes *Carallia*, *Gynotroches* and *Pellacalyx* as well as other members with inferior or half-inferior ovary, small embryo embedded in fleshy albumen of the seed and opposite stipulate leaves.
- (3) the *Anisophylleae*, including *Anisophyllea* and *Combretocarpus* with inferior ovary, 3–4 styles, exalbuminous macropodous embryo, and alternate stipulate leaves.

Schimper's proposed classification is altogether different; an outline of it follows:

- (1) *Rhizophoroideae* — includes genera with perigynous or epigynous flowers, simple styles, baccate or rarely capsular fruits, opposite, stipulate leaves.
 - (a) *Gynotrocheae* — comprising two sub-tribes.
 - (i) *Gynotrochinae* — consisting of *Crossostylis*, *Gynotroches*, *Ceriops*, *Kandelia* and *Rhizophora*.
 - (ii) *Carallinae* — composed of *Carallia*, *Pellacalyx* and *Bruguiera*.
 - (b) *Macarisieae* — comprising *Blepharistemma*, *Cassipourea*, *Dactylopetalum*, *Macarisia* and *Weihea*.
- (2) *Anisophylloideae* — including genera with epigynous flowers, 3–4 styles, drupaceous or dry indehiscent fruits, alternate, exstipulate leaves. Only two genera, *Anisophyllea* and *Combretocarpus* are included in this sub-family.

Among the genera belonging to Hooker's Legnotidae, Schimper found that certain members, namely, *Weihea*, *Cassipourea*, *Blepharistemma*, *Dactylopetalum* and *Macarisia*, are so distinctly related that he placed them in a tribe of their own, *Macariseae*, to which he later assigned *Anopyxis* and *Sterigmapetalum*. The remaining genera he placed with the mangrove species.

According to Hooker, the mangrove genera are placed in a group of their own because of the several distinctive characters they exhibit, the majority of which are no doubt of adaptive significance and origin. On this very point Schimper (1898) voices his dissent, and considers it erroneous to separate a group of plants on the strength of their response to environmental conditions. He favours a 'natural' classification which gives a more realistic indication of the relationships of the plants within the family. The outcome of his proposal is the dispersion of the mangrove genera into two different sub-tribes of *Gynotrocheae*, each of which includes some of the inland genera.

Hooker's proposal of a third tribe Anisophylleae was accepted, but relegated to a sub-family by Schimper.

Ridley agreed with Hooker's arrangement of the Rhizophoraceous genera, but raised all the three tribes to family rank. In his investigation he found that the inland genera *Carallia*, *Gynotroches* and *Pellacalyx* are closely related and warrant a group of their own. Other members of Hooker's Legnotidae were not investigated as his study was confined to the Malayan flora, and hence Schimper's suggestion of the Macarisieae as a distinct tribe was not discussed.

He also assigned *Anisophyllea* to a separate family Anisophylleaceae (as Anisophylleae), and this was later taken up by Corner (1952).

In the latest (12th) edition of Engler's Syllabus as revised by Melchior (in Melchior 1964), the family Rhizophoraceae is divided into four co-ordinated tribes as follows: Macarisieae, Gynotrocheae, Anisophylleae and Rhizophoreae.

In the present investigation of the Rhizophoraceous genera found in Johore, Malaysia, and in Singapore, some morphological data have been assembled and tabulated (see Table 6) in the three tribes proposed by Hooker (1898) but revised by Melchior (1964). On the strength of the morphological features it appears that these three tribes resemble one another very closely in many ways but yet have their distinct differences. The mangrove tribe differs from the inland counterparts not exclusively but manifestly in their ecological adaptive features.

TABLE 6

COMPARISON OF SOME MORPHOLOGICAL CHARACTERS OF THE 3 TRIBES OF RHIZOPHORACEAE

<i>Rhizophoreae</i> (<i>Rhizophora</i> , <i>Bruguiera</i> , <i>Ceriops</i>)	<i>Gynotrocheae</i> [Legnotideae] (<i>Carallia</i> , <i>Gynotroches</i> <i>Pellacalyx</i>)	<i>Anisophylleae</i> (<i>Anisophyllea</i> , <i>Combretocarpus</i>)
1. Trees of littoral habitats.	1. Trees of inland forests.	1. Trees of inland forests.
2. Leaves opposite, entire, glabrous.	2. Leaves opposite, entire or serrate, glabrous or densely puberulous.	2. Leaves alternate, entire, glabrous to pubescent.
3. Stomata anomocytic.	3. Stomata anomocytic.	3. Stomata anomocytic.
4. Stipules present.	4. Stipules present.	4. Stipules absent.
5. Phellogen subepidermal in origin.	5. Phellogen subepidermal in origin.	5. Phellogen subepidermal in origin.
6. Flowers medium-sized to large (0.5–4 cm.)	6. Flowers small to medium-sized (0.25–1.5 cm.)	6. Flowers minute (0.15–0.5 cm.)
7. Calyx lobes persistent; 4–15 in number.	7. Calyx lobes persistent; 4–8 in number.	7. Calyx lobes persistent; 3–4 in number.
8. Petals entire or lobed, with or without appendages.	8. Petals clawed, fringed at the apex in various degrees.	8. Petals laciniate or entire.
9. Stamens twice the number of petals or numerous, equal or unequal in length.	9. Stamens twice the number of petals, usually unequal in length.	9. Stamens twice the number of petals, equal or unequal in length.

TABLE 6—continued

COMPARISON OF SOME MORPHOLOGICAL CHARACTERS OF THE 3 TRIBES OF RHIZOPHORACEAE

<i>Rhizophoreae</i> (<i>Rhizophora</i> , <i>Bruguiera</i> , <i>Ceriops</i>)	<i>Gynotrocheae</i> [Legnotideae] (<i>Carallia</i> , <i>Gynotroches</i> , <i>Pellacalyx</i>)	<i>Anisophylleeae</i> (<i>Anisophyllea</i> , <i>Combretocarpus</i>)
10. Anthers basifixed, multi-loculate or 4-locular.	10. Anthers basifixed, 4-locular.	10. Anthers basifixed 4-locular.
11. Filaments shorter or longer than anthers.	11. Filaments several times longer than anthers.	11. Filaments several times longer than anthers.
12. Disc present or absent.	12. Disc present.	12. Disc present.
13. Pollen grains $24\ \mu - 26\ \mu$ in longest axis.	13. Pollen grains $12\ \mu - 15\ \mu$ in longest axis.	13. Pollen grains $20\ \mu - 24\ \mu$ in longest axis.
14. Carpels 1–4; ovary half-inferior or inferior, syncarpous.	14. Carpels 3–12; ovary superior or inferior, syncarpous.	14. Carpels 3–5; ovary inferior, syncarpous.
15. Ovules 2–6 per locule.	15. Ovules 2–several per locule, fasciculate or not.	15. Ovules 1–2 per locule.
16. Fruit a specialized structure with seed which germinates while still attached to parent plant.	16. Fruit a berry, usually globose or pyriform.	16. Fruit a drupe or dry and indehiscent with winged or woody pericarp.
17. Pericarp hard and tough.	17. Pericarp succulent.	17. Pericarp succulent or dry.
18. Seeds one per fruit.	18. Seeds numerous, embedded in pulpy placentae in fruit.	18. Seeds one per fruit.
19. Endosperm absent.	19. Endosperm present.	19. Endosperm present.
20. Embryo macropodous; cotyledons connate or free.	20. Embryo minute, embedded in fleshy endosperm; cotyledons free.	20. Embryo macropodous. cotyledons rudimentary or not.

The following discussions are centrated on the three tribes as proposed by Hooker but revised by Melchior.

(A) *On the tribe Rhizophoreae*

The Rhizophoraceae may be conveniently divided into mangrove and inland groups on ecological grounds. Members of the former group belong to the tribe Rhizophoreae, those of the latter, to the tribes Gynotrocheae (or Legnotidae) and Anisophylleeae. In spite of Schimper's (1898) strong objection to the adoption of this scheme, the mangrove genera (namely, *Rhizophora*, *Bruguiera*, *Ceriops* and *Kandelia*) in many aspects, do form a closely related unit. The development of such characters as xerophytic leaves, prop roots, pneumatophores, in mangrove plants are undoubtedly brought about as a result of ecological adaption. However, there are many other features such as persistent and accrescent sepals, ex-endospermous seed and wood anatomical characters which set this tribe apart.

The unique method of viviparous germination of seeds in the Rhizophoreae seems to be another adaptive feature. However, as van Steenis (in Hou, 1958) pointed out, it is not universal or even common in other equally successful mangrove plants such as *Sonneratia* (Sonneratiaceae) or *Barringtonia* (Barringtoniaceae), thus the general assumption that this character is a special adaption to the environment may be disputable.

(B) *On the tribe Gynotrocheae*

In the tribe Gynotrocheae (= Legnotidae, in part) only 3 genera, namely, *Carallia*, *Gynotroches* and *Pellacalyx* were studied. They appear to fit into a natural group. However, according to Marco (1935), this tribe is heterogeneous, and therefore should be further divided into 3 groups: (1) Group I including *Carallia*, *Combretocarpus*, *Anisophyllea*, *Gynotroches* and *Crossostylis*, (2) Group II including *Macarisia* and four other genera which are not present in this part of the world, (3) Group III including *Pellacalyx* and *Poga*. Unfortunately most of this material are not available for the present study.

It is noted that Marco's Groups I and II correspond closely to Schimper's tribes Gynotrocheae and Macariseae. Marco (1935) also considered *Pellacalyx* to be wood anatomically unclassifiable with the others. Although this genus differs in its tangential arrangement of 2–5 vessels in pore clusters, and in the possession of opposite, angular pits to ray cells, yet with regard to the other wood anatomical characters, it seems to fit in homogeneously with the rest of the Gynotrocheae. Therefore it would appear to be unwarranted to separate *Pellacalyx* out solely on these points of difference.

(C) *On the tribe Anisophylleeae*

Anisophyllea and *Combretocarpus*, which constitute the Anisophylleeae, are conspicuous by the alternate arrangement of their leaves as contrasted to the paired condition found in the other tribes, and by their lack of the characteristic interpetiolar stipules of the family. The flowers of these two genera are very tiny by comparison, their 3–4 styles are free, yet the fruits produced are relatively large to very large (for example, 8–12 × 5–7 cm in *Anisophyllea grandis* Burk.). Anatomically, *Anisophyllea* shows a tendency towards formation of isolateral leaves without a hypoderm, and has less palisade tissues than the other inland genera. Transverse sections of the young stem show the presence of a sheath of sclerenchymatous cells surrounding the vascular cylinder, which is not found in the other genera examined. These features are probably among the deciding factors for the separation of the two genera, *Anisophyllea* and *Combretocarpus*, into a tribe or even into a family as advocated by Ridley (1922) and Corner (1952).

The embryos in the seeds of the Anisophylleeae resemble those of the Rhizophoreae in being macropodous. Other common features between these two tribes include the deeply bi-lobed petals and the comparatively larger size of the pollen grains. The wood anatomical characters of the Anisophylleeae on the other hand, in general, agree very well with those of the Gynotrocheae, but appear to be more advanced. For example, they possess shorter, broader vessel elements than *Carallia*, *Gynotroches* and *Pellacalyx* (of Gynotrocheae), and the pores are larger, often solitary and fewer in number. Therefore, on morphological grounds it would hardly seem justifiable to establish a separate family to accommodate these two genera.

To summarize, after due consideration of the data available, it appears to be most appropriate that the Malayan members of the family Rhizophoraceae should be accommodated in three tribes: namely Rhizophoreae, Gynotrocheae and Anisophylleae, as suggested by Hooker (1865) and revised by Melchior (1964).

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Plate 1. Flowering branches. A, B, *Carallia brachiata* (Lour.) Merr. C, D, *Pellacalyx axillaris* Korth. (Scale: A, B and D, 1 cm. divisions; C, 1 mm. divisions).

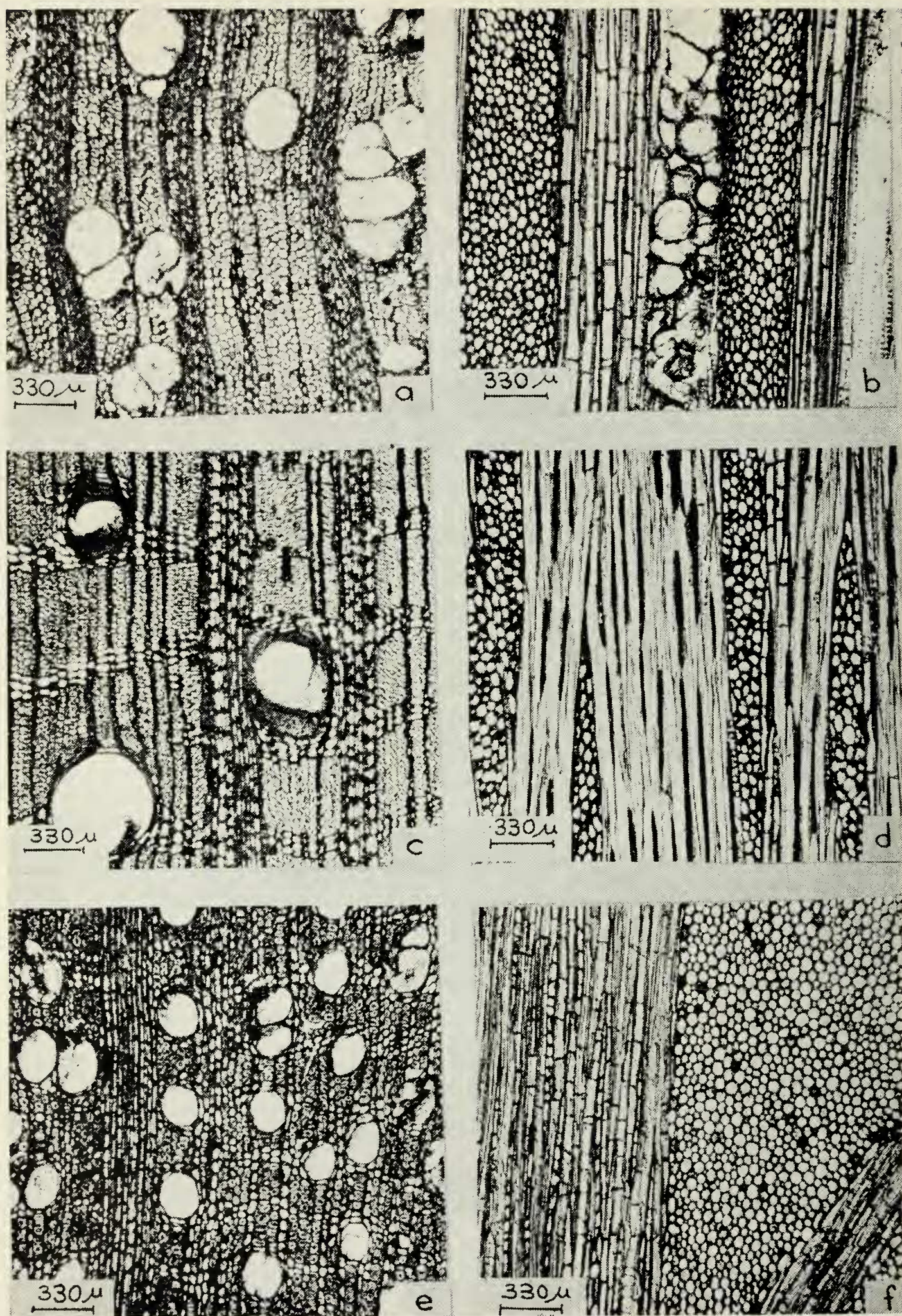


Plate 2. Wood anatomy. *Carallia brachiata*: a, TS. b, TLS. *Combretocarpus rotundatus*: c, TS. d, TLS. *Gynotroches axillaris*: e, TS. f, TLS.

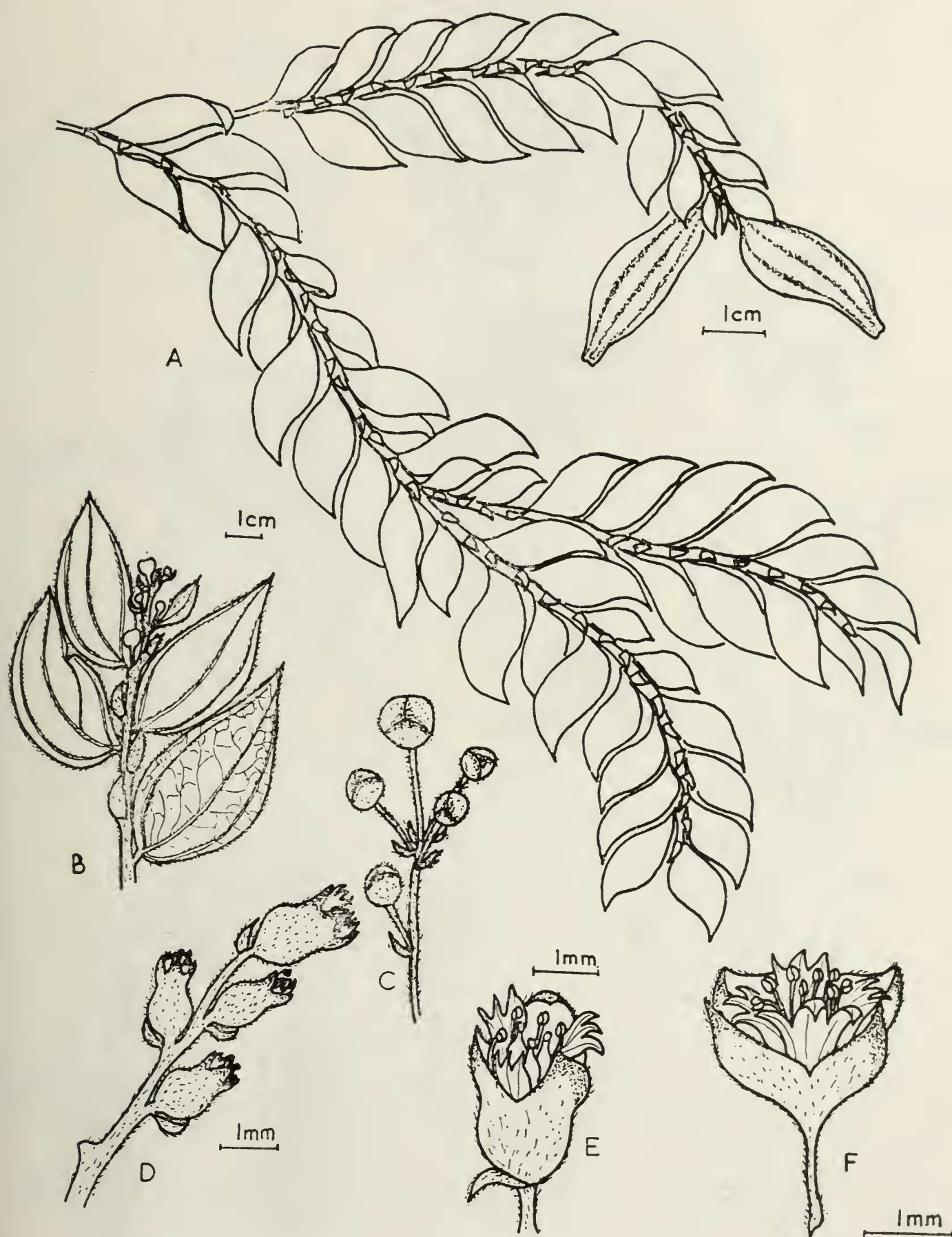


Figure 1. *Anisophyllea disticha* Baill.: A, pendent lateral branch bearing a pair of fruits. B, flowering branch. C, male inflorescence. D, female inflorescence. E, female flower. F, male flower.

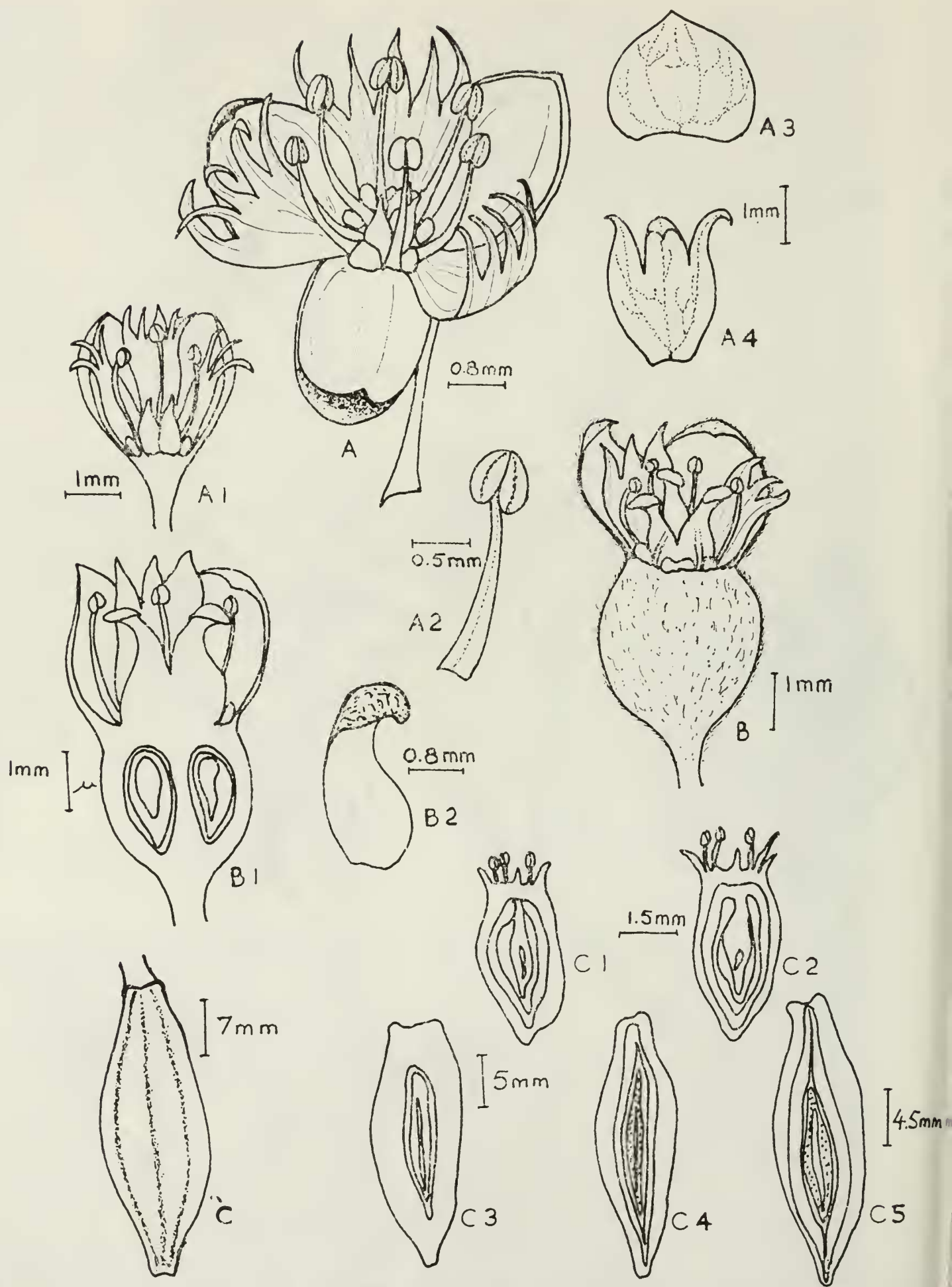


Figure 2. *Anisophyllea disticha* Baill.: A, male flower. A1, half-flower (male). A2, stamen. A3, Sepal. A4, petal. B, female flower. B1, half-flower (female). B2, style and stigma. C, mature fruit, C1-C5, longisections of various stages in fruit development.

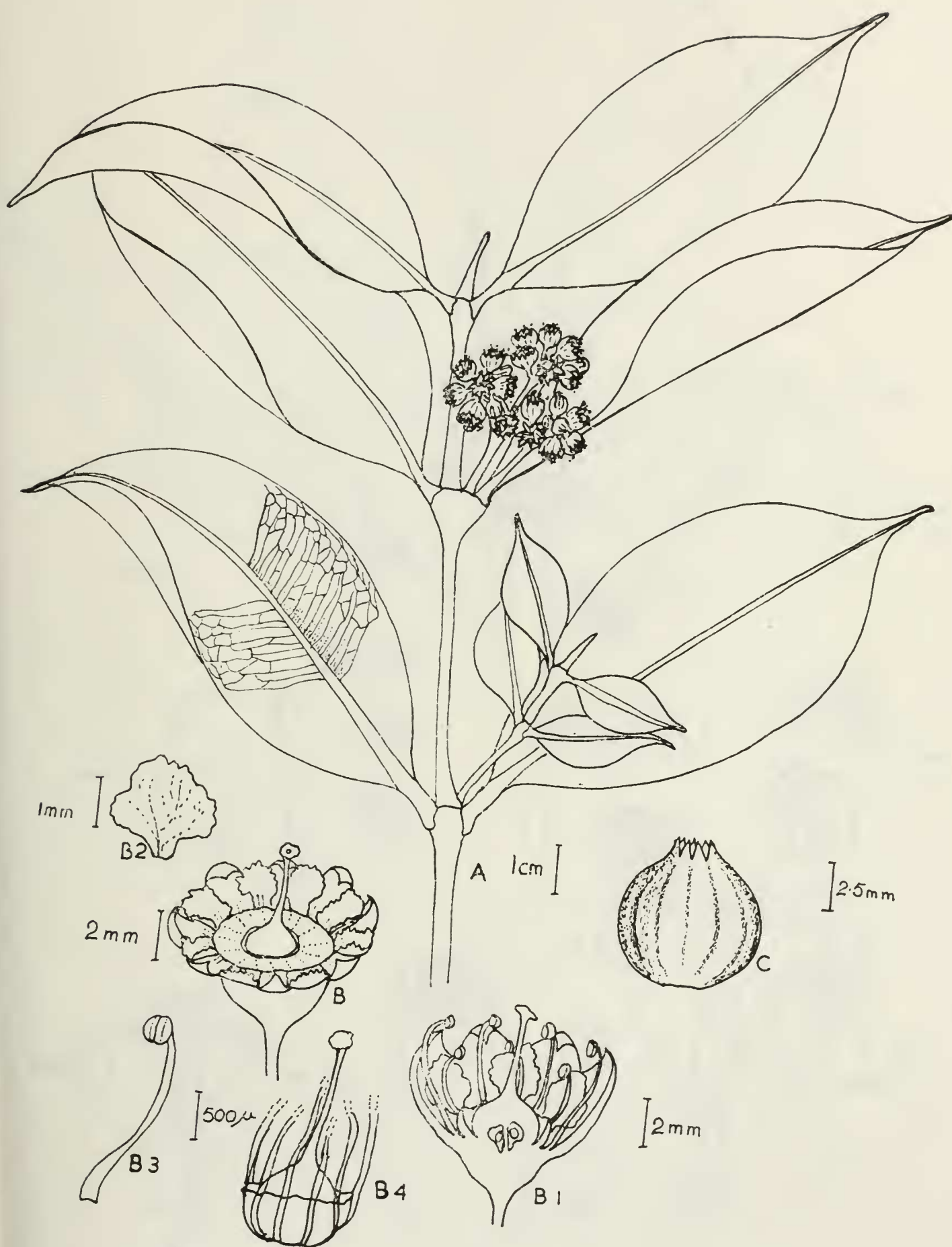


Figure 3. *Carallia brachiata* (Lour.) Merr.: A, flowering branch. B, flower with stamens removed. B1, half-flower. B2, petal. B3, stamen. B4, ovary with surrounding disc and attached filaments. C, fruit.

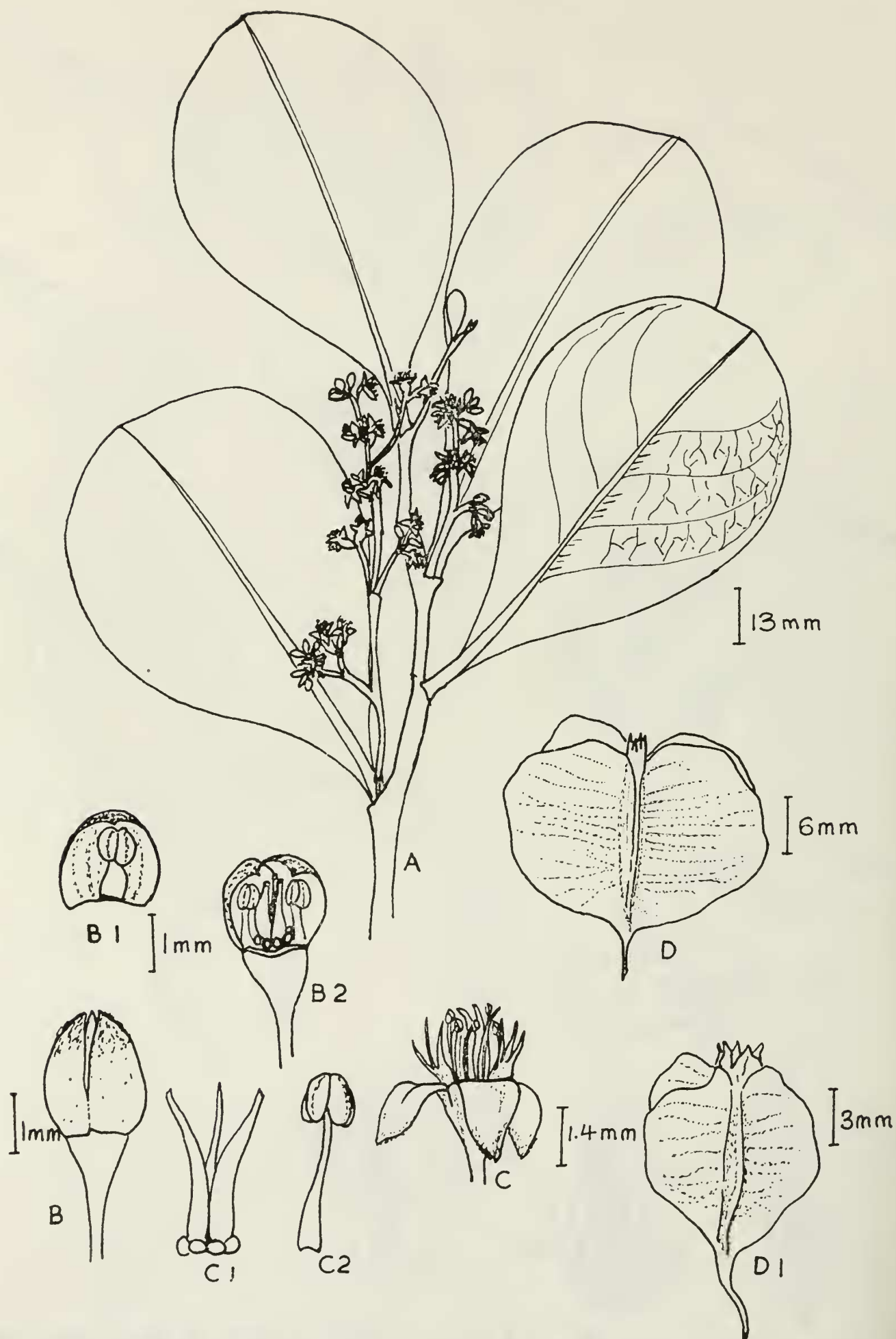


Figure 4. *Combretocarpus rotundatus* (Miq.) Danser: A, flowering branch. B, flower bud. B1, sepal and antisepalous stamen. B2, flower bud with petals and one sepal removed to show stamens, lobed disc and styles. C, mature flower. C1, style and stigma with surrounding, deeply lobed disc. C2, stamen. D, mature fruit. D1, younger fruit.

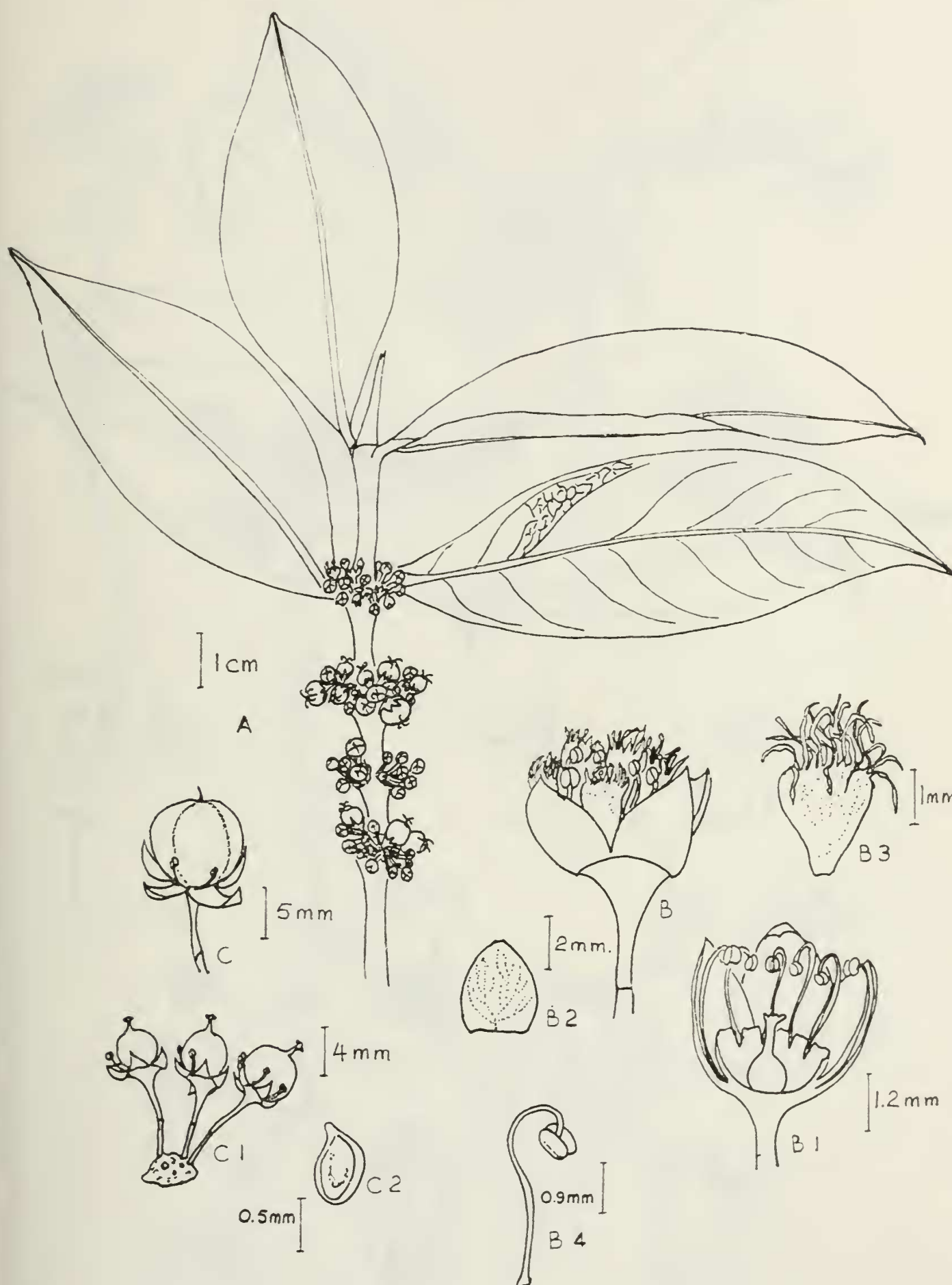


Figure 5. *Gynotroches axillaris* B1.: A, flowering and fruiting branch. B, flower. B1, half-flower. B2, sepal. B3, petal with apical appendages. B4, stamen. C, fruit with basal persistent calyx. C1, cluster of fruits. C2, seed.

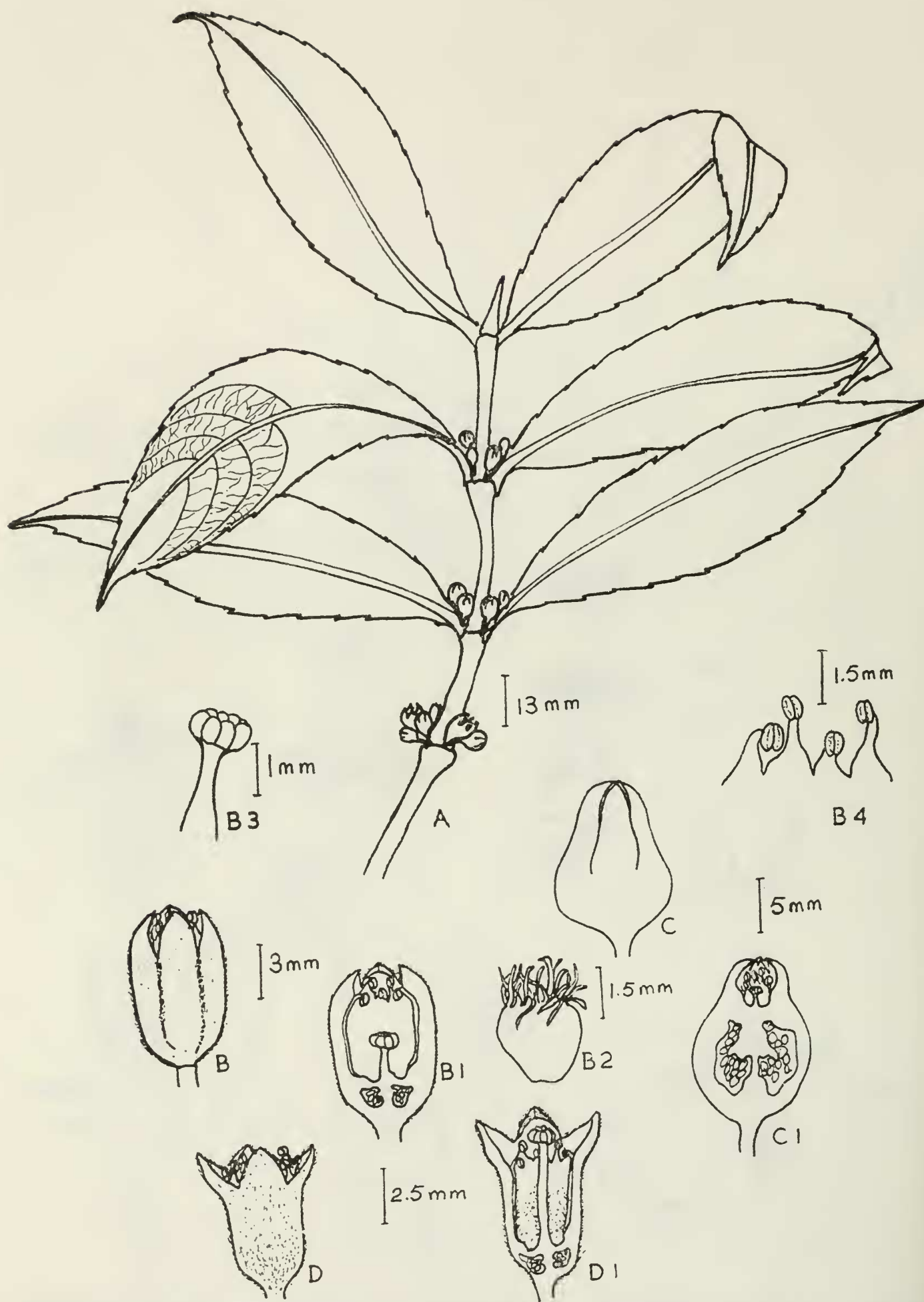


Figure 6. *Pellacalyx saccardianus* Scort.: A, flowering branch; B, flower, B1, half-flower, B2, petal, B3, style and lobed stigma, B4, stamen, C, fruit, C1, longitudinal section of fruit. *P. axillaris* Korth.: D, flower, D1, half-flower.

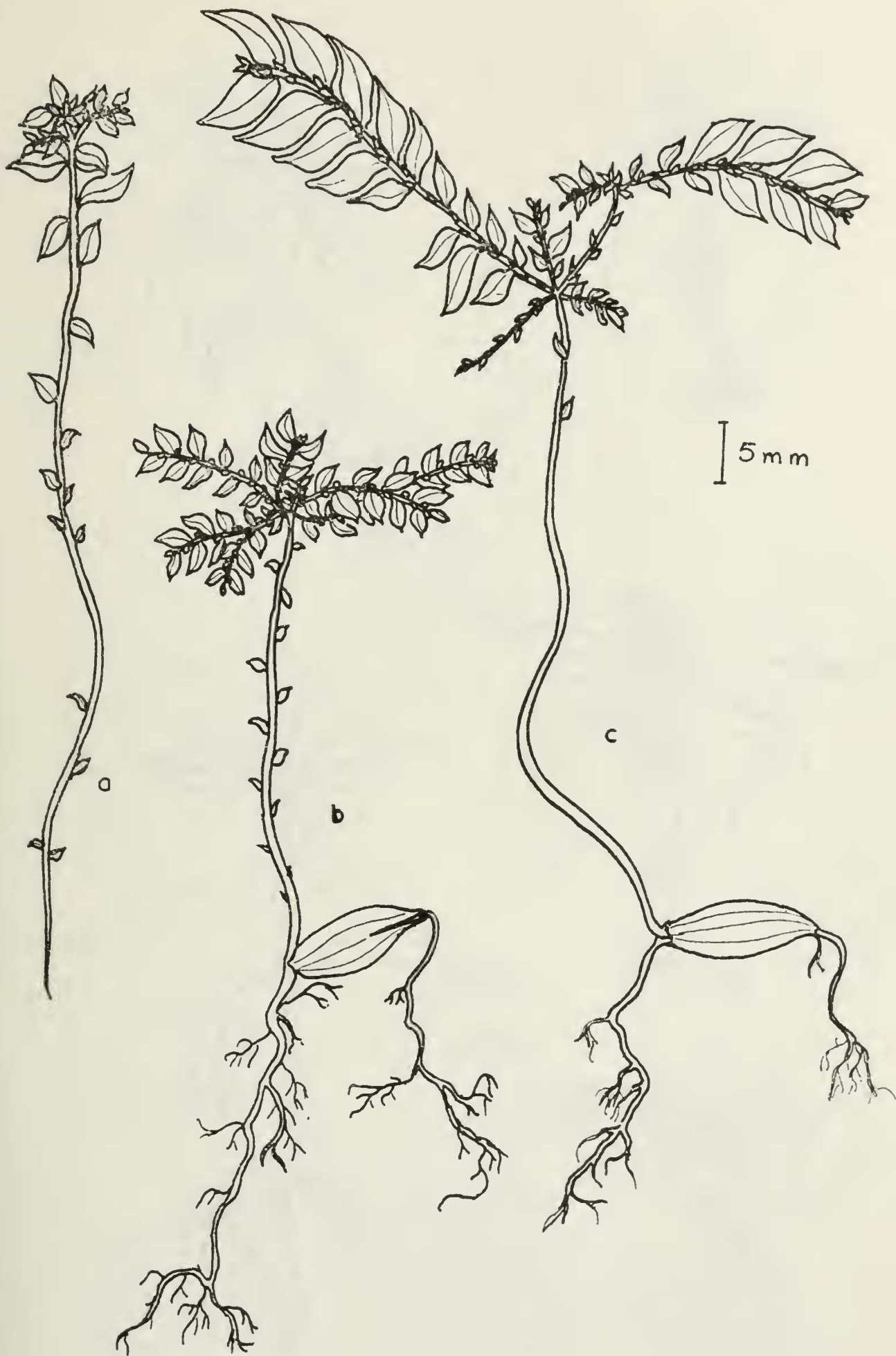


Figure 7. *Anisophyllea disticha* Baill.: a-c, progressive stages in seedling development. Stages b and c show the remains of the fruit which is embedded in the soil. Roots arise from both ends of the fruit.

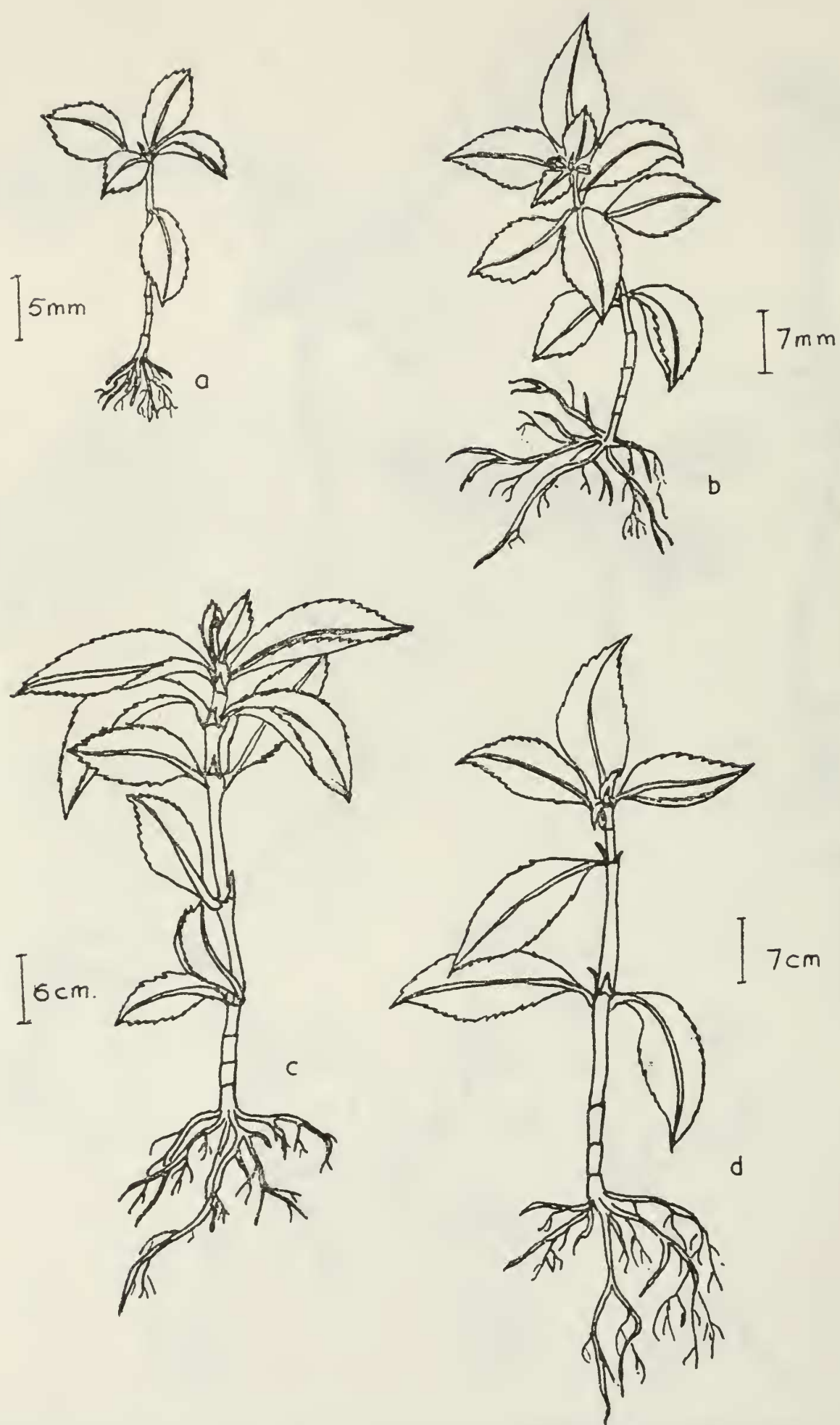


Figure 8. *Gynotroches axillaris* Bl.: a-d, stages in seedling development.

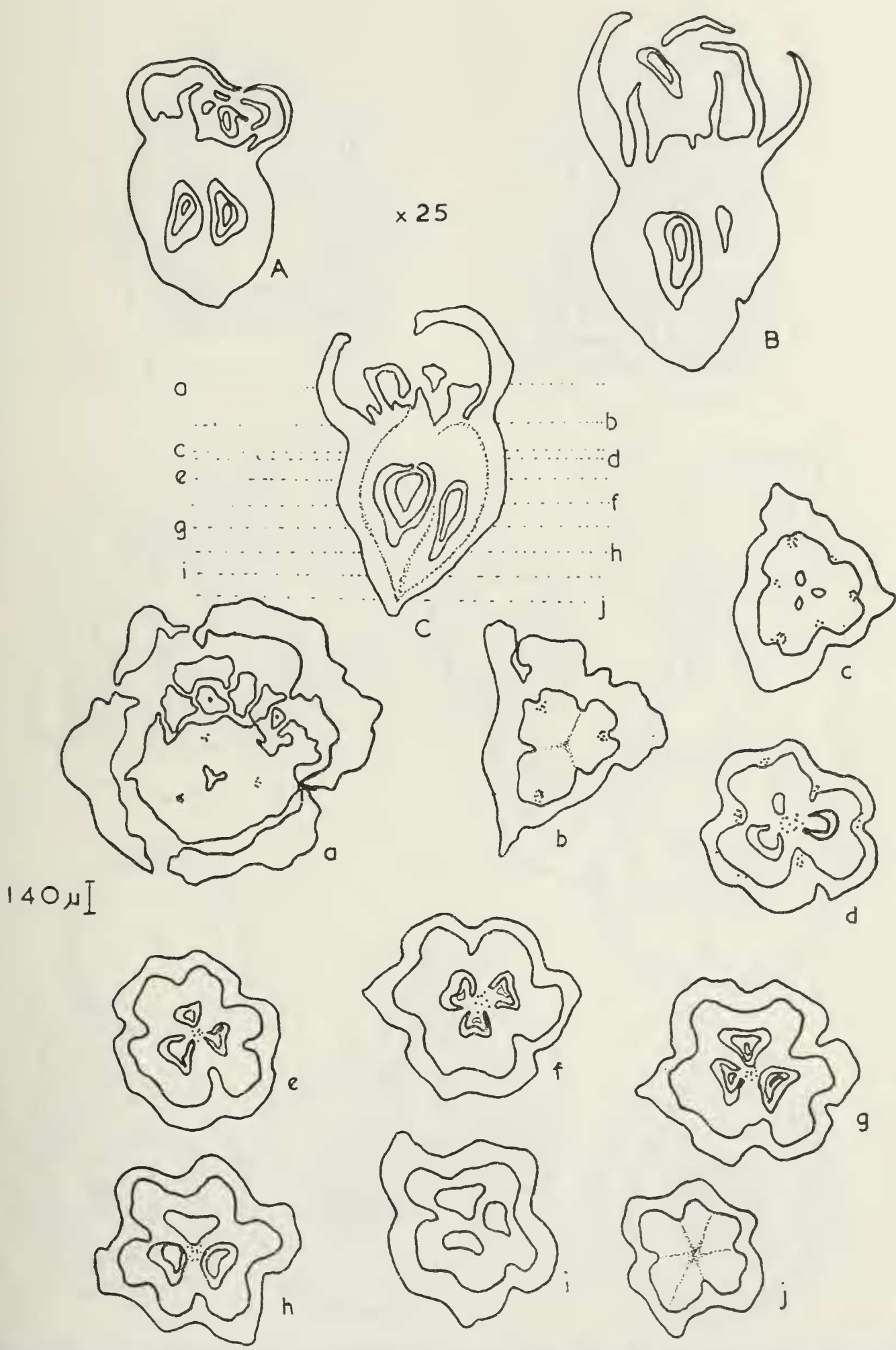


Figure 9. *Anisophyllea disticha* Baill.: A, B & C, different longitudinal sections of female flower. a-j, transections at different levels as indicated in C.

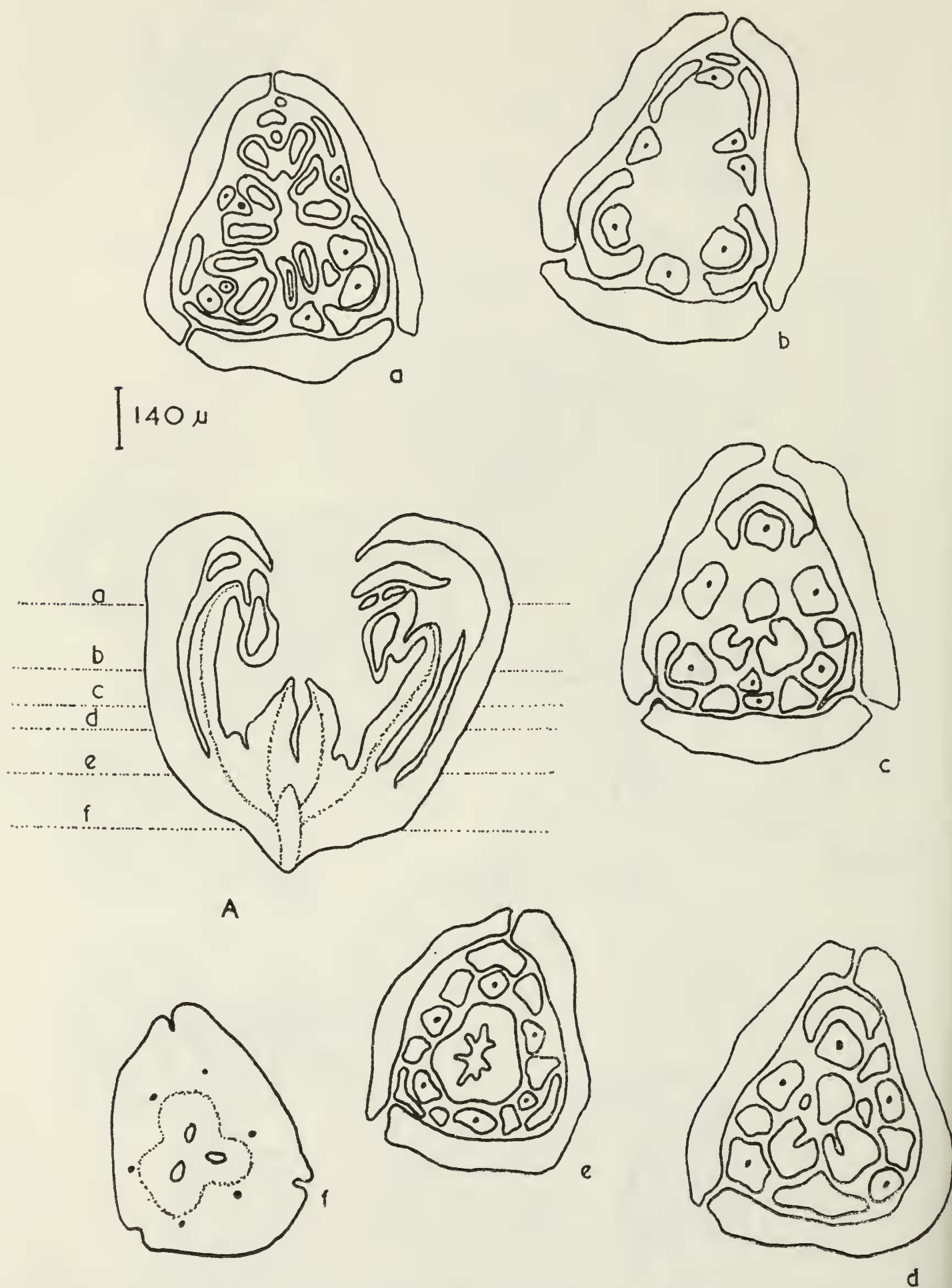


Figure 10. *Anisophyllea disticha* Baill.: A, longisecton of male flower. a-f, transverse sections at levels indicated in A.

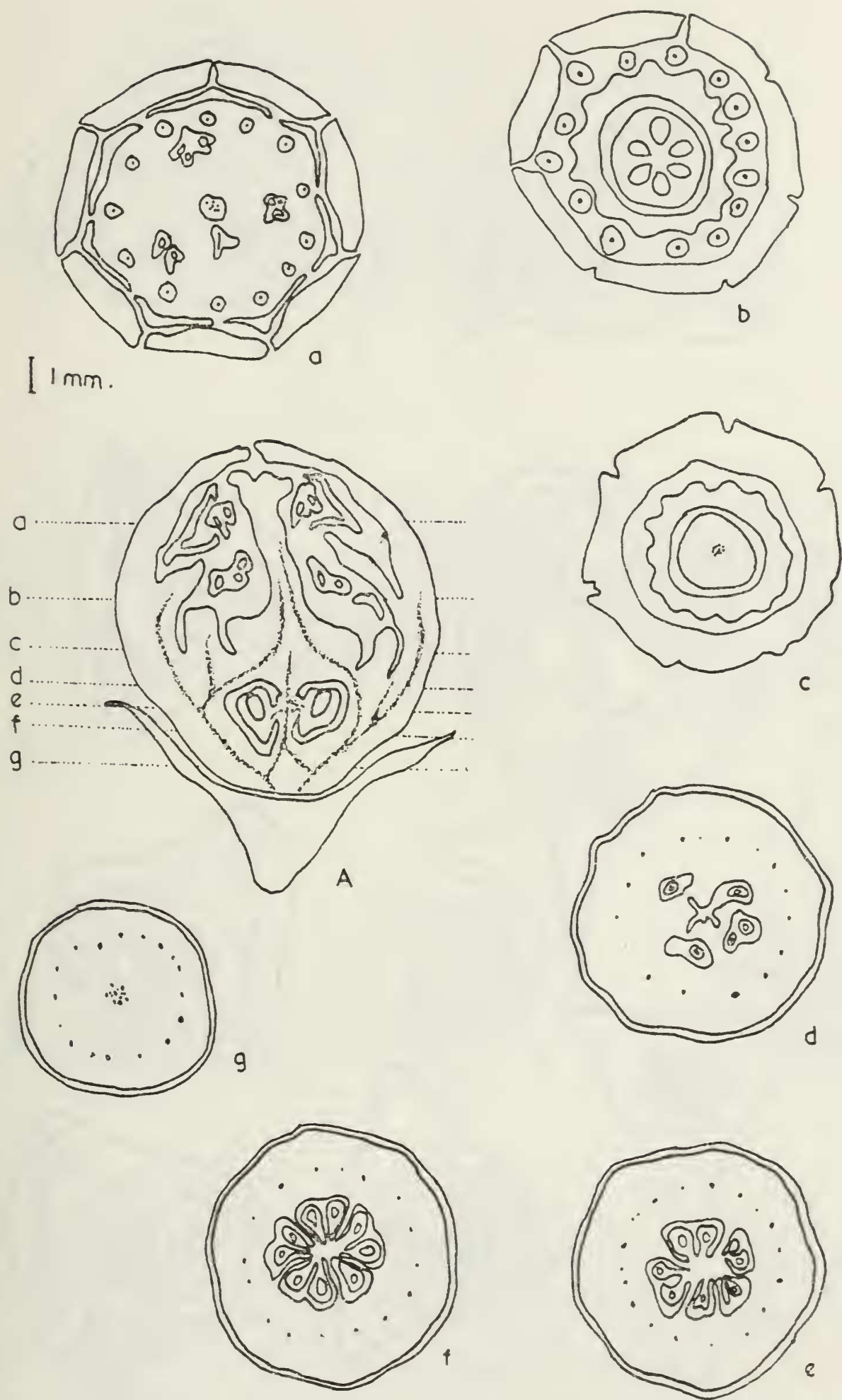


Figure 11. *Carallia brachiata* (Lour.) Merr.: A, longitudinal section of flower. a-g, transverse sections at levels corresponding to those shown in A.

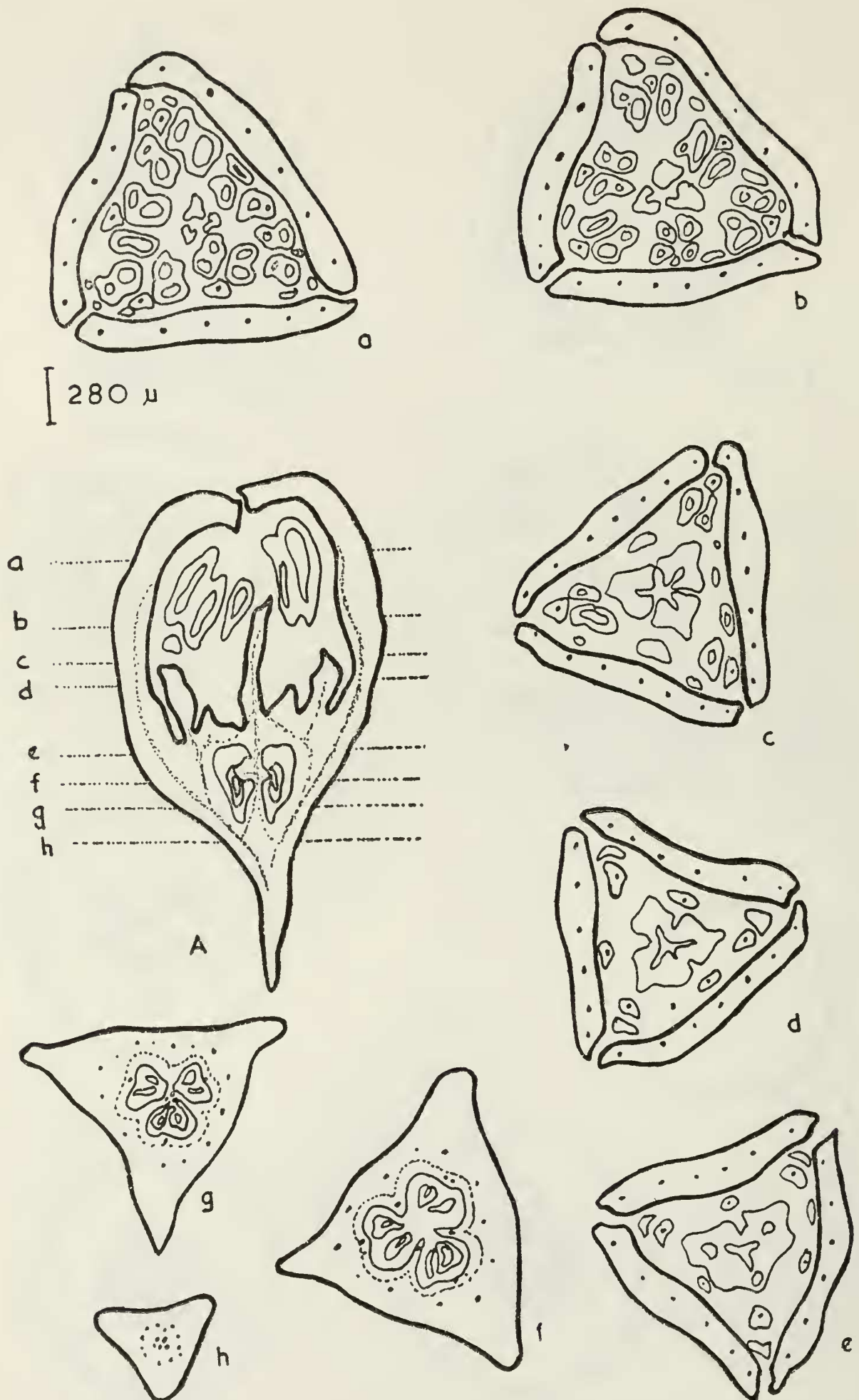


Figure 12. *Combretocarpus rotundatus* (Miq.) Danser: A, longisection of flower, a-h, transverse sections at levels shown in A.

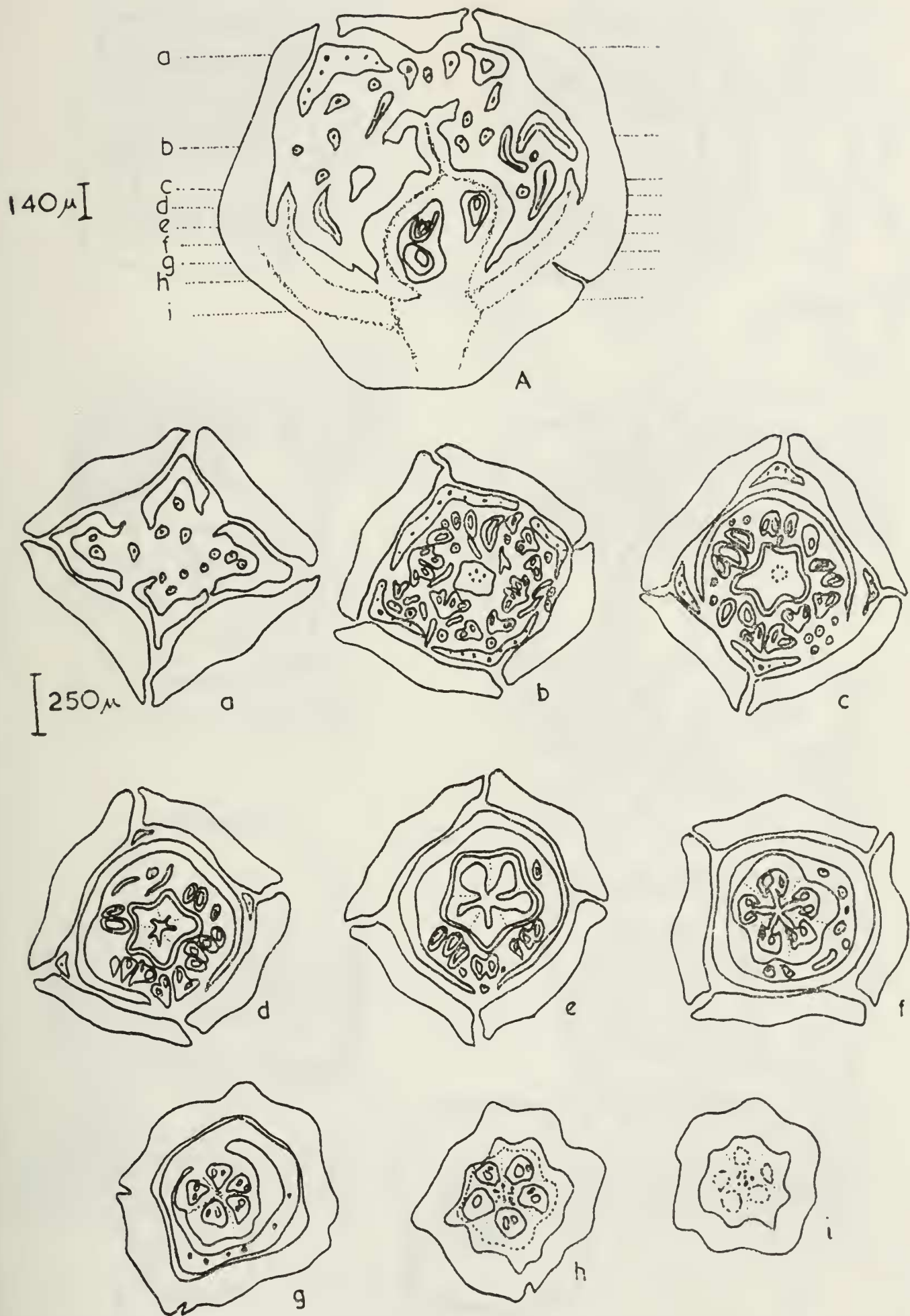


Figure 13. *Gynotroches axillaris* Bl.: A, longitudinal section of flower, a-i, transverse sections at different levels.

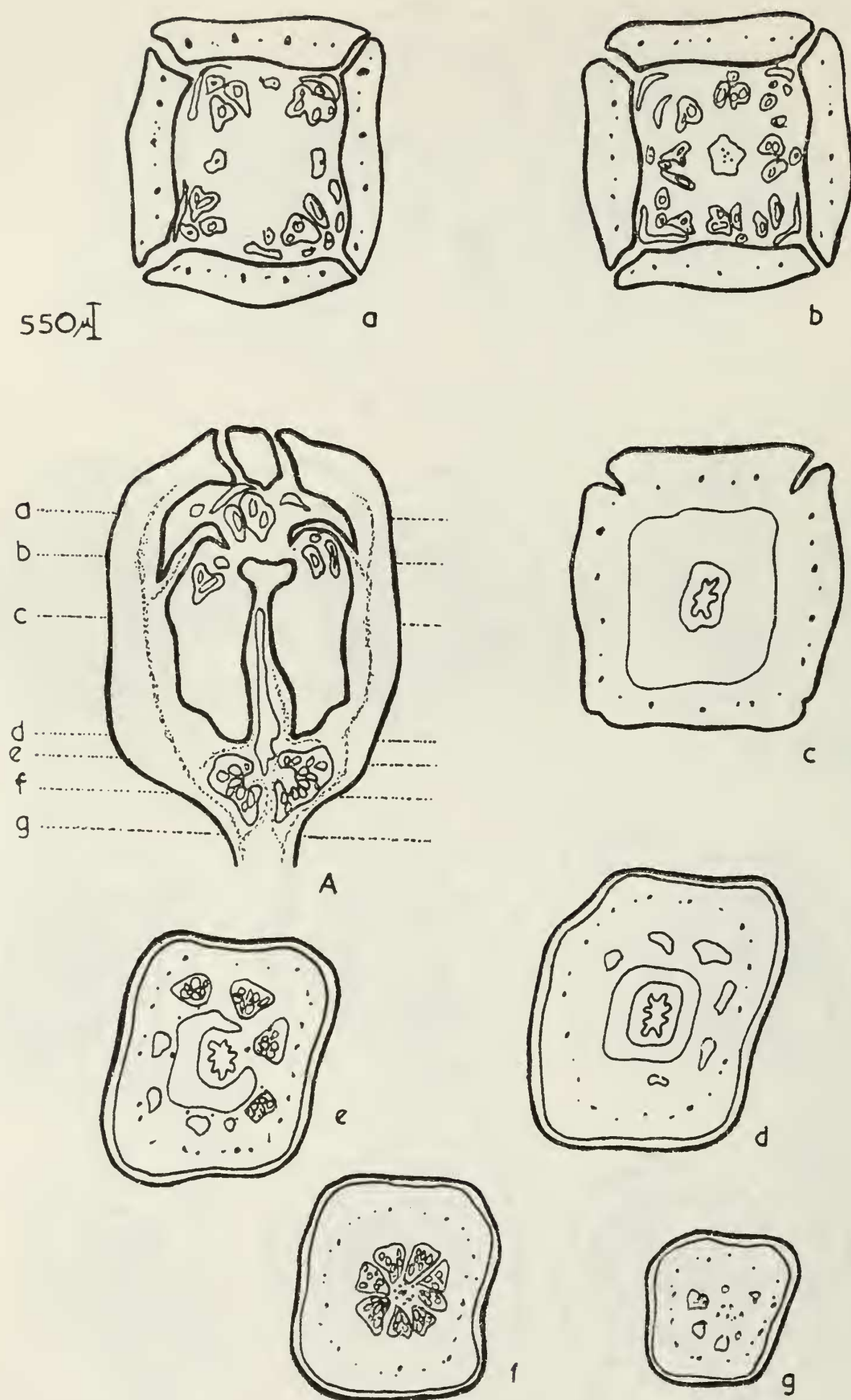


Figure 14. *Pellacalyx saccardianus* Scort.: A, longitudinal section of flower. a-g, transections of flower at levels indicated in A.

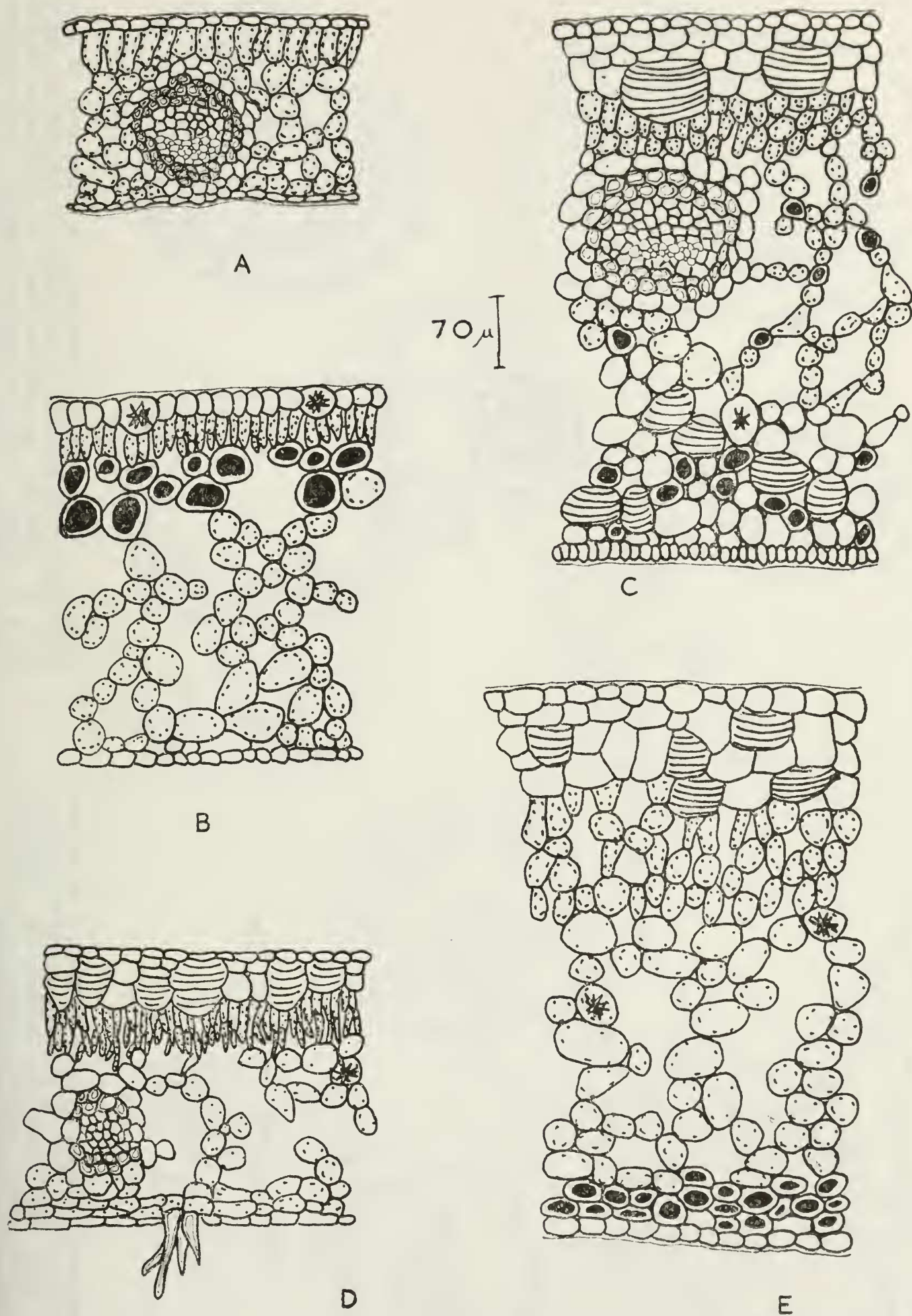


Figure 15. Transverse section of leaves. A, *Anisophyllea disticha* Baill. B, *Carallia brachiata* (Lour.) Merr. C, *Gynotroches axillaris* Bl. D, *Pellacalyx axillaris* Korth. E, *P. saccardianus* Scort. Mesophyll cells stippled to represent chlorenchymatous condition. Amorphous cell inclusions, heavy black. Mucilage-producing cells are hatched.

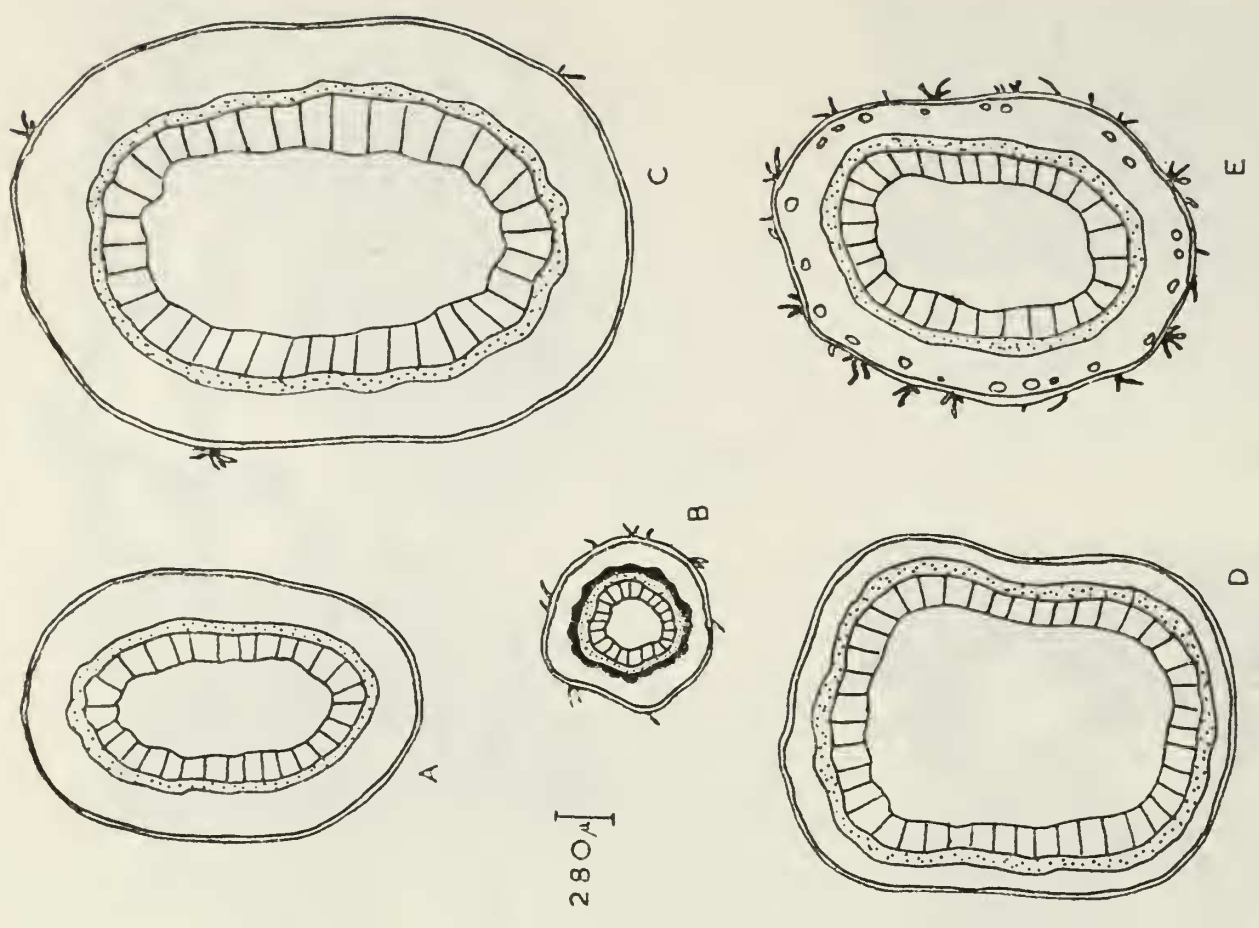


Figure 17. Diagrammatic representation of transverse sections of young stems. A, *Carallia brachiata* (Lour.) Merr. B, *Anisophyllea disticha* Baill. C, *Pellacalix saccardianus* Scort. D, *Gynotroches axillaris* Bl. E, *P. axillaris* Korth, with mucilage-producing cells in peripheral region. (hatched = xylem, stippled = phloem, heavy black = sclerenchyma).

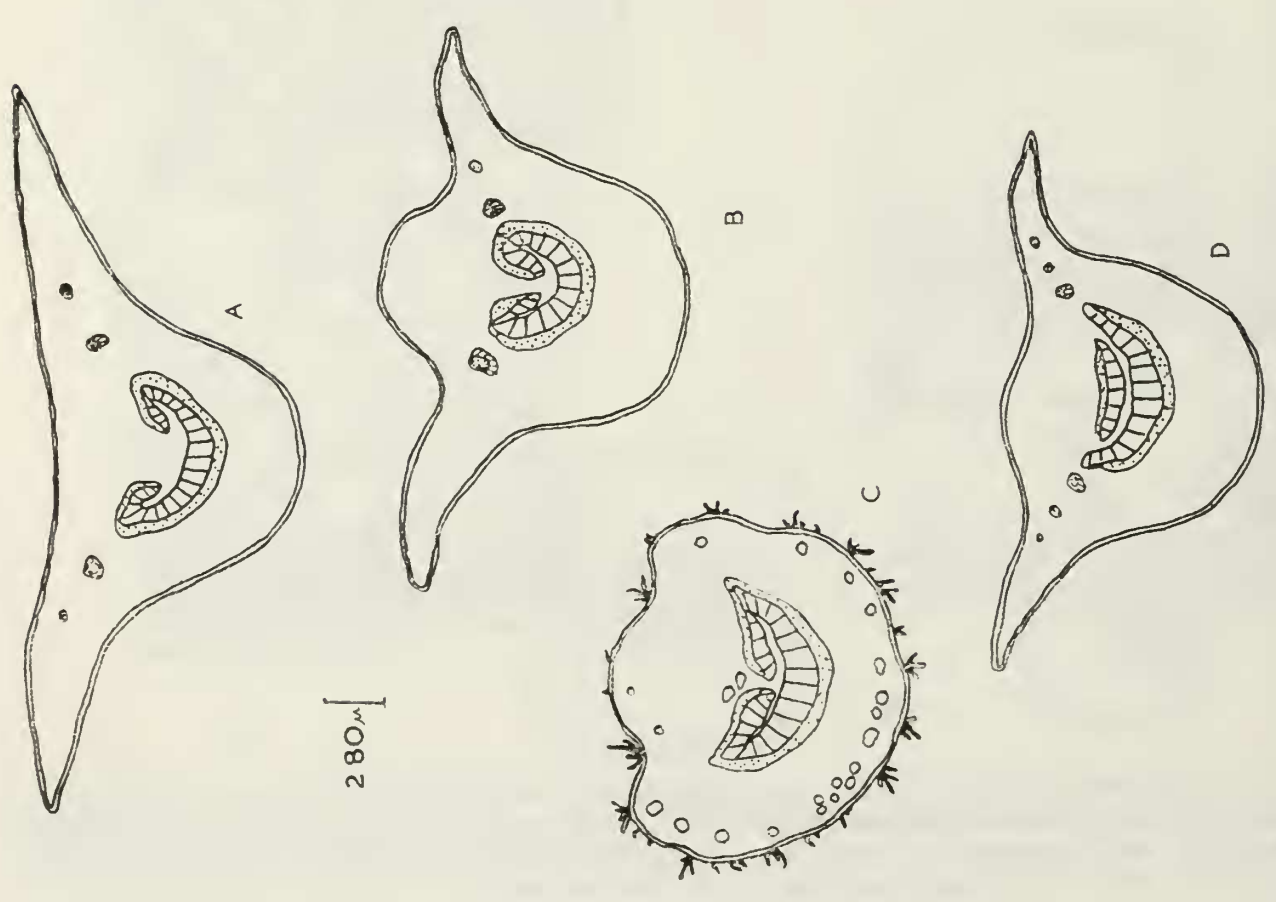


Figure 16. Diagrammatic representation of transverse sections of petioles. A, *Carallia brachiata* (Lour.) Merr. B, *Pellacalix saccardianus* Scort. C, *P. axillaris* Korth. D, *Gynotroches axillaris* Bl. Mucilage-producing cells present around peripheral region of petiole of *P. axillaris* Korth. (stippled = xylem, hatched = phloem).